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Entyloma eranthidis* sp. nov. on *Eranthis longistipitata

(Denchev & al.— FIG. 2, p. 379)

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Corrigenda for Mycotaxon 136(2)

Cited below are mistakes present in files submitted for PDF conversion in the current issue but not detected by the authors until after the paper had gone to press.

p. 533, line 2
for: C. Section of context; D. Lower surface pores; ...
read: C. Lower pores surface; D. Pores section under microscope; ...

p. 533, line 3
for: I. Binding hyphae J. ...
read: I. Binding hyphae; J. ...

p. 537, line 1 for: The 5–6 mm long tubes *G. leucocontextum* ...
read: The 5–6 mm long tubes of *G. leucocontextum* ...

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Mycotaxon *for* January–March 2021 (i–xvi + 1–262)
was issued on April 16, 2021

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[IF 556182] p. 341
Collybiopsis brunneigracilis (Corner) R.H. Petersen
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≡ *Agaricus ramealis* Bull. 1788 nom. sanct.,
[IF 556205, (epitypified)], p. 326
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[MB 835127], p. 427
≡ *Ionaspis tropica* Aptroot 1997, nom. illegit.
(non Riddle 1920)
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[IF 557827], p. 404
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[MB 834624], p. 353
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[MB 834626], p. 353
Pseudosperma albobrunneum Jabeen, Zainab, H. Bashir & Khalid
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Reviewers — volume one hundred thirty-six (2)

The Editors express their appreciation to the following individuals who have, prior to acceptance for publication, reviewed one or more of the papers prepared for this issue.

Andreas Beck
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Tibpromma Saowaluck
Steven L. Stephenson
Priyanka Uniyal
Else C. Vellinga
Nousheen Yousaf
Juan Carlos Zamora
Chang-Lin Zhao

From the Editor-in-Chief

Late again? — We could write volumes explaining why Mycotaxon 136(2) is delayed. But rather than spew meaningless ink on these pages, we simply offer a brief apologetic explanation: the 2021 April–June Mycotaxon is being released in July/August because: the EIC foolishly thought she might prepare her own research paper after closure of 136(1), medical issues and side effects assaulted both editors after April, Oregon melted under a record-breaking June "heat dome" (on June 30 reaching a high 116°F (46.7°C) with no air-conditioning and hot nights), the editorial Adobe publishing application began disintegrating, with InDesign stalling several times daily and finally snatching carefully formatted tables or eating italics from text in front of horrified editorial eyes, and the Internet crashed. Internet service was restored last week. After repeated crashes, the frazzled EIC uninstalled and reinstalled all Adobe applications, imported and formatted missing text and italics anew, restored tables, and more or less successfully converted the final five papers confronting a VERY strange interface. (Some time in the past four years, the Adobe subscription disappeared off the editorial computer, to be replaced by a rickety 2013 application. Don't ask. The EIC's First Born is convinced the editorial computer is haunted. We see no evidence to the contrary.)

A Mycotaxon primer to scientific names: Undergraduates are generally taught that a scientific name comprises two elements: the name of the genus (capitalized) + the name of the species (all lower case): e.g., *Russula campinensis*. In mycological taxonomic journals, scientific authors are also expected to cite authorities (generally only once): i.e., *Russula campinensis* (Singer) T.W. Henkel, Aime & S.L. Mill. Authors cited within parentheses are those who originally named the species while those standing outside the brackets transferred the species to a different genus. A species name that serves as the title of a section containing a full description heads a 'taxonomic section' and includes the complete taxonomic reference: genus name, species name, naming authors, an abbreviated but complete bibliographic reference, and date of publication. The complete taxonomic reference of the name above is: *Russula campinensis* (Singer) T.W. Henkel, Aime & S.L. Mill., Mycologia 92(6): 1124 (2000).

Basically, we cite authorities only once per paper to make the text more user friendly. If a species is not part of a taxonomic heading, authorities are cited generally at first mention. Because now complete fungal names (including bibliographic reference) are available on the internet, the Code recommends (for 'incidental' mention in a taxonomic paper) that species named by more than two authors be cited as First author & al. (i.e., *Russula campinensis* (Singer) T.W. Henkel & al.).

Index Fungorum also presents a list of standardized author spellings: see http://www.indexfungorum.org/names/AuthorsOfFungalNames.asp . Reference to this list will ensure that each authority is spelled consistently in mycological literature. When in doubt how to present a taxonomic heading, use IndexFungorum (universally available online) as a model.

One last note: although names of synonyms and basionyms are nomenclatural in nature, the decision as to which synonym should be used is a taxonomic (NOT nomenclatural) decision.

Our 2021 April–June Mycotaxon provides 17 contributions by 70 authors (representing 17 countries) as revised by 35 expert reviewers and the editors.

The New taxa (6 titles) section leads off the issue with a monographic treatment of *Collybiopsis,* here endorsed over *Marasmiellus* "especially by (re)describing taxa within the *Co. ramealis* complex with emphasis on European collections of *Co. ramealis;*" the authors propose five new species (one a previously described taxon here elevated to species), and 35 new combinations. New taxa also covers one new genus (*Parathozetella* from Brazil) and an additional four species new to science representing *Entyloma* from Uzbekistan; *Kirschsteiniothelia* from India; *Parathozetella* from Brazil; and *Pseudosperma* from Pakistan. We also offer two new combinations in *Calogaya* and *Huneckia* and one epitypification for *Collybiopsis* (≡ *Agaricus*) *ramealis.*

Keys presents an impressive key to the 258 genera of lichenized fungi in Thailand, which also proposes the replacement name *Ionaspis aptrootii* for the illegitimate *I. tropica*.

New ranges/hosts (seven titles) report range extensions for [ascomycetes] *Camarosporidiella* for Italy, Ukraine, and Russia and *Geopora* for Pakistan; [basidiomycetes] *Chlorophyllum* and *Ganoderma* for Pakistan and *Microbotryum* for Nepal; [lichens] *Didymocyrtis, Lichenochora,* and *Lichenoconium* for Turkey; and [myxomycetes] *Dictyostelium* for China. New hosts are cited for *Camarosporidiella* from Ukraine.

Papers providing research supported by phylogenetic analysis include seven new species representing *Collybiopsis, Entyloma,* and *Pseudosperma*, the two new *Calogaya* and *Huneckia* combinations, and nine range extensions.

Our issue concludes with the announcement of two new annotated species lists on our mycobiota website, covering lichenized fungi from the Amazon (Brazil) and basidiomycetes within Calabrian pine ecosystems on Cyprus.

Warm (no longer hot!) regards and best wishes for good health,
Lorelei L. Norvell (*Editor-in-Chief*)
21 July 2021

2021 Mycotaxon submission procedure

Prospective Mycotaxon authors should download the Mycotaxon 2021 guide, review & submission forms, and Mycotaxon sample manuscript by clicking the 'file download page' link on our Instructions to Authors page before preparing their manuscript. This page briefly summarizes our '4-step' submission process.

1—Peer review: Authors first contact peer reviewers (two for journal papers; three for mycobiota/fungae) before sending them formatted text & illustration files and the appropriate 2021 Mycotaxon journal or mycota reviewer comment form. Experts return revisions & comments to both the *Editor-in-Chief* <editor@mycotaxon.com> and authors. All co-authors must correct and *proof-read* their files before submitting them to the *Nomenclature Editor*.

2—Nomenclatural review: Authors email all **error-free** text & illustration files to the *Nomenclature Editor* <PennycookS@LandcareResearch.co.nz>. Place **first author surname** + **genus** + 'Mycotaxon' on the subject line, and (required) attach a completed submission form. The Nomenclature Editor will (i) immediately assign the accession number and (ii) after a few weeks return his notes and suggested revisions to the author(s) and *Editor-in-Chief*.

3—Final submission: All coauthors thoroughly revise and proof-read files to prepare error-free text and images ready for immediate publication. Poorly formatted copy will be rejected or returned for revision. E-mail the final manuscript to the *Editor-in-Chief* <editor@mycotaxon.com>, adding the **accession number** to the message and **all** files, which include a (**i**) revised 2021 submission form, all (**ii**) text files and (**iii**) jpg images, and (**iv**) FN, IF, or MB identifier verifications for each new name or typification. The *Editor-in-Chief* acknowledges submissions within two weeks of final submission but requests authors to wait at least 14 days before sending a follow-up query (without attachments).

4—Final editorial review & publication: The *Editor-in-Chief* conducts a final grammatical and scientific review and returns her editorial revisions to all expert reviewers and coauthors for final author approval. Author-approved files are placed in the publication queue.

The PDF proof and bibliographic & nomenclatural index entries are sent to all coauthors for final inspection. After PDF processing, the *Editor-in-Chief* corrects only PDF editorial/conversion and index entry errors; corrections of all other errors are listed in the Errata of a subsequent issue for no charge. Authors will pay fees for mycobiota uploads, optional open access, and correction of major author errors to the *Business Manager* <subscriptions@mycotaxon.com> at this time.

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Collybiopsis and its type species, *Co. ramealis*

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Abstract—*Collybiopsis* (*Omphalotaceae*, *Agaricales*) is accepted as the correct genus name for a large clade of non-typical *Gymnopus*. The type species of *Collybiopsis* (*Agaricus ramealis*) is shown to be a genetic complex. *Collybiopsis filamentipes*, *Co. furtiva*, *Co. hasanskyensis*, and *Co. minor* are proposed as spp. nov. and *Co. californica* as a stat. nov. Thirty-four additional *Collybiopsis* comb. nov. are proposed in Appendix I.

Key words—clade /marasmiellus, morphology, taxonomy, new combinations, new species

Introduction

For many years, agaric taxonomists have dealt with the morphological and molecular diversity of both *Gymnopus* and *Marasmius*. Several segregate genera have been carved from *Gymnopus*, but a large complex of fungi remains, comprising taxa contributed by elements of *Gymnopus*, *Marasmius*, and *Marasmiellus*. This large assemblage has been called *Marasmiellus* (see Wilson & Desjardin 2005), presumably because the type species of *Marasmiellus*, *Ma. juniperinus*, is included. Recent papers by Dutta & al. (2015) and Oliveira & al. (2019) are among the latest to draw attention to *Marasmiellus*. Two principles were included: 1) presentation of a well-populated phylogeny to demonstrate placement of numerous taxa exhibiting "gymnopoid," "marasmioid," and/or "marasmielloid" taxonomic character suites; and 2) the use of the genus name *Marasmiellus* to represent a large taxonomic group that includes type species of at least two genera (*Marasmiellus* and *Collybiopsis*) plus taxa of *Gymnopus* sect. *Vestipedes*. While

we agree with the taxonomy presented, we choose to follow the International Code of Nomenclature (Turland & al. 2018, Art. 11.3) in accepting the prior genus name, *Collybiopsis*, for the group that Oliveira & al. (2019) and Wilson & Desjardin (2005) called *Marasmiellus*.

Nomenclaturally, *Collybiopsis* Earle 1909 (with its explicit type species *Agaricus ramealis* Bull. 1787) has clear priority over *Marasmiellus* Murrill 1915 (explicitly typified by *Ma. juniperinus* Murrill). Use of *Marasmiellus* for this clade would require conservation of this genus name, not yet proposed. In addition, *Ma. juniperinus* is poorly represented phylogenetically (two ITS-based sequences, neither from the topotype location). Conversely, *Co. ramealis* is a well-known taxon molecularly represented from original topotype locales. The relative placement of these taxa is shown in Figs 1, 2. To our knowledge, only Horak (1971) has recombined basionyms into *Collybiopsis*.

Taxonomic circumscription of fungi assigned to *Marasmiellus*-like taxa has changed and enlarged over the last century. Although an extensive literature chronology could be narrated, this is not the intent of this paper. Instead, literature can be concisely cited, leaving further investigation to the reader. A sketch of this morpho-taxonomic process includes: Antonín & Noordeloos (1993, 1997, 2010); Clements & Shear (1931, 1954); Corner (1996); Donk (1962); Earle (1909); Horak (1968); Kühner (1933, 1936); Murrill (1915); Patouillard (1900); Singer [1936, 1945, 1948, 1962—dismissing *Collybiopsis* and accepting *Marasmiellus* with 59 species; for more on this, see "Discussion"—and 1973 with 134 species listed in *Marasmiellus*]. Since the introduction of molecular tools in fungal taxonomy, numerous papers have presented phylogenetic trees including or alluding to the group under consideration. These papers include Aldrovandi & al. (2015); Binder & Hibbett (2002); Dentinger & al. (2016); Desjardin (1997); Desjardin & al. (2017); Desjardin & Perry (2017); Dutta & al. (2015); Honan & al. (2015); Hughes & Petersen (2015); Hughes & al. (2001, 2008); Kerekes & Desjardin (2009); Kim & al. (2015); Mata & al. (2004, 2007); Matheny & al. (2006); Moncalvo & al. (2000, 2002); Nakasone & al. (2009); Oliveira & al. (2019); Petersen & Hughes (2014, 2016, 2017a,b); Sandoval-Leiva & al. (2016); and Wilson & Desjardin (2005).

The intent of this paper is to endorse use of *Collybiopsis* over *Marasmiellus*, especially by (re)describing taxa within the *Co. ramealis* complex with emphasis on European collections of *Co. ramealis*. A list of proposed transfers into *Collybiopsis* appears in Appendix I.

TABLE 1. Collections used in phylogenetic analyses. (HT = holotype; ET = epitype)

ORGANISM	HERBARIUM NO.	ISOLATE	LOCATION	FIG. NO.	GENBANK ITS	GENBANK LSU
Collybiopsis biformis						
Co. biformis	TENN-F-068109	TFB14251	USA: Tennessee, GSMNP	1	KJ416245	KJ189567
Co. biformis	TENN-F-68108	TFB14250	USA: Tennessee, GSMNP	1	KJ416246	KJ189568
Co. biformis	TENN-F-065586	TFB13890	USA: North Carolina	1	KJ416248	KJ189570
Co. biformis	TENN-F-065189	TFB13814	USA: Tennessee	1	KJ416249	KJ189569
Collybiopsis brunneigracilis						
Co. brunneigracilis	AWW01-SFSU	AWW01	Java/Bali	1	AY263434	AY639412
Collybiopsis californica						
Co. californica	Environmental	—	USA: California	1, 2	DQ273359	—
Co. californica	Environmental	—	USA: Oregon	1, 2	HM488468	—
Co. californica	Environmental	—	USA: Oregon	1, 2	HM488469	—
Co. californica	SFSU: Wright866	Wright866	USA: California	1, 2	MN413335	—
Co. californica	SFSU-F-024539	Wright2941	USA: California	1, 2	MN413336	—
Co. californica	SFSU-F-024526	DED8372	USA: California	1, 2	MN413337	—
Co. californica	TENN-F-052617	TFB5787	Canada: British Columbia	1, 2	MN413338	—
Collybiopsis confluens* ssp. *americana						
Co. confluens ssp. *americana* [HT]	TENN-F-069073	TFB14409	Canada: New Brunswick	1	KP710278	KJ189585
Co. confluens ssp *americana*	TENN-F-069053	TFB14389	Canada: New Brunswick	1	KP710279	KJ189584
Co. confluens ssp *americana*	TENN-F-067822	TFB14075	USA: North Carolina	1	KP710281	KJ189581
Collybiopsis confluens						
Co. confluens	TENN-F-067865	TFB14115	Germany, Thuringia	1	KP710292	KJ189578
Co. confluens	TENN-F-067864	TFB14114	Germany, Thuringia	1	KP710296	KJ189573
Collybiopsis dichroa						
Co. dichroa	TENN-F-056721	TFB10009	USA: North Carolina	1	KY026654	KY026654
Co. dichroa	TENN-F-067859	TFB14111ss1	USA: Tennessee, GSMNP	1	KY026696	KY026696
Co. dichroa	TENN-F-067859	TFB14111ss2	USA: Tennessee, GSMNP	1	KY026697	KY026697
Co. dichroa	TENN-F-056584h1	TFB9623	USA: North Carolina	1	MW396865	MW396865
Co. dichroa	TENN-F-056584h2	TFB9623	USA: North Carolina	1	MW396866	MW396866

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Co. dichroa	TENN-F-065569	TFB13873	USA: North Carolina	1	MW396867	MW396867
Co. dichroa	TENN-F-051775	TFB5459	USA: South Carolina	1	MW396868	MW396868
Co. dichroa	TENN-F-048680	TFB1860	USA: North Carolina	1	MW396869	MW396869
Collybiopsis disjuncta						
Co. disjuncta	TENN-F-068136	TFB14281	USA: Mississippi	1	KJ416253	KY019643
Co. disjuncta [HT]	TENN-F-069172	TFB14339	USA: Connecticut	1	NR_137865	—
Collybiopsis eneficola						
Co. eneficola	TENN-F-069122	10-09-021AV04	Canada: Newfoundland	1	KJ128265	KJ189590
Co. enificola	MICH:PK6975	PK6975	Alaska	1	KP710270	KP710304
Co. enificola	MICH:PK6975	PK6976	Alaska	1	KP710271	KP710305
Co. eneficola [HT]	TENN-F-069123	09-09-26AV13	Canada: Newfoundland	1	NR_137613	NG_059502
Collybiopsis filamentipes						
Co. filamentipes	environmental	KTRF390	Canada: Alberta	1	MG433317	
Co. filamentipes	TENN-F-065861	TFB13962	USA: Tennessee	1	MN897832	MN897832
Collybiopsis foliiphila						
Co. foliiphila	CUM AM101	—	India	1	KP317638	KP317636
Co. foliiphila [HT]	CUH AM090	—	India	1	NR_154176	NG_060320
Collybiopsis furtiva						
Co. furtiva as M. ramealis	SFSU: DED4425	DED4425	USA: North Carolina	2	DQ450031	AF042650
Co. furtiva	SFSU-F-024523	DED3973	USA: North Carolina,	1, 2	MN413339	—
Co. furtiva	SFSU-F-024508	DED4584	USA: North Carolina	1, 2	MN413340	—
Co. furtiva	SFSU-F-024524h1	DED5796h1	USA: North Carolina	1, 2	MN413341	—
Co. furtiva	SFSU-F-024524h2	DED5796h2	USA: North Carolina	1, 2	MN413342	—
Co. furtiva (as Marasmiellus)	TENN-F-051097	TFB4796	USA: Georgia	1, 2	MN413343	MW396879
Collybiopsis gibbosa						
Co. gibbosa	MEL:2382838	—	Australia	1	KP012713	KP012713
Co. gibbosa	URM 90012	—	Brazil	1	KY061202	KY061202
Co. gibbosa	URM 90006	—	Brazil	1	KY061203	KY061203
Collybiopsis hasanskyensis						
Co. hasanskyensis	TENN-F-060730	TFB11846	Russia: Kedrovaya	1	MN897829	—
Co. hasanskyensis	TENN-F-060731	TFB11847	Russia: Kedrovaya	1	MN897830	—

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Collybiopsis juniperina						
Co. juniperina	TENN-F-059540	TFB9889	USA: Louisiana	1	AY256708	KY019637
Co. juniperina	TENN-F-058988	TFB10782	Argentina: Missiones	1	KY026661	KY026661
Collybiopsis luxurians						
Co. luxurians	TENN-F-057910	TFB10350	USA: North Carolina	1	AY256709	AY256709
Co. luxurians	TENN-F-050619	TFB4283ss10	Sweden	1	KJ416240	—
Co. luxurians	TENN-F-055748	TFB9121	USA: Louisiana	1	KY026649	KY026649
Co. luxurians	TENN-F-067806	TFB14060	USA: North Carolina	1	MW396871	MW396871
Collybiopsis melanopus						
Co. melanopus	CUH AM093	—	India	1	KM896875	KP100305
Co. melanopus [HT]	SFSU: AWW54	AWW54	Java/Bali	1	NR-137539	NG_060624
Collybiopsis menehune						
Co. menehune [HT]	SFSU: DED5866 Holotype	—	Hawaii	1	AY263426	—
Co. menehune	SFSU-AWW15	—	Java/Bali	1	AY263443	AY639424
Co. menehune	Culture only	TFB11587, D. E. Hemmes 2320	Hawaii	1	DQ450043	—
Co. menehune	CUH AM089	—	India	1	KJ778753	KP100306
Collybiopsis mesoamericana						
Co. mesoamericana	NYBG:REH7379	REH7379	Costa Rica	1	AF505768	—
Co. mesoamericana	TENN-F-058106	TFB10411	Costa Rica	1	DQ450036	—
Co. mesoamericana [HT]	TENN-F-058613 Type	TFB11005	Costa Rica	1	NR_119583 = DQ450035	KY019632
Collybiopsis minor						
Co. minor	TENN-F-059993	TFB11930	USA: Tennessee, GSMNP	1, 2	MN413334	MW396880
Co. minor	TENN-F-051792	TFB5434	USA: South Carolina	1, 2	MW396872	MW396872
Co. minor	TENN-F-052933	TFB6284	USA: South Carolina	1, 2	MW405778	—
Collybiopsis neotropica						
Co. neotropica	TENN-F-058110	TFB10416	Costa Rica	1	AF505769	—
Collybiopsis nonnulla						
Co. aff *nonula*	TENN-F-068085	TFB14492	USA: Mississippi	1	KY026699	KY026699

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Co. aff *nonula*	TENN-F-068133	TFB14278	USA: Mississippi	1	KY026701	KY026701
Collybiopsis nonnulla var attenuatus						
Co. nonnulla v *attenuata*	SFSU: AWW05	AWW05	Java/Bali	1	AY263445	AY639426
Co. nonnulla v *attenuata*	SFSU: AWW55	AWW55	Java/Bali	1	AY263446	—
Co. nonnulla v *attenuata*	—	RAK369.2	Cameroon	1	MN930621	—
Co. nonnulla v *attenuata*	—	RAK372.2	Cameroon	1	MN930622	—
Co. obscuroides						
Co. obscuroides	GB-0150514	—	Norway: Svalbard	1	KX958399	KX958399
Co. obscuroides	GB-005381	—	Sweden: Jamtland	1	KX958498	KX958498
Collybiopsis parvula						
Co. parvula	TENN-F-058116	TFB10422	Costa Rica	1	AF505774	—
Co. parvula	TENN-F-058115	TFB10421	Costa Rica	1	DQ450061	—
Co. parvula	TENN-F-058119	TFB10425	Costa Rica	1	DQ450062	—
Co. parvula as *Marasmiellus parvulus*	—	SR83-10MX	Mexico	1	KT697977	—
Co. parvula as *G.* sp. VC-2017k	URM 90054		Brazil	1	KY404984	
Co. parvula [HT]	TENN-F-058113	TFB10419	Costa Rica	1	NR_119584.1 = DQ450060	—
Collybiopsis peronata						
Co. peronata	UBCF28402		Canada: British Columbia	1	KP454027	—
Co. peronata	TENN-F-065120	TFB13743	Belgium	1	KY026677	KY026677
Co. peronata	Culture only	LE-Bin1364	Russia	1	KY026755	KY026755
Co. peronata as Gymnopus peronatus	CBS 223.37	—	unknown	1	MH855896	MH867405
Collybiopsis polygramma						
Co. polygramma	TENN-F-056589	PR2542TN	Puerto Rico	1	AY842954	—
Co. polygramma	TENN-F-056589	TFB9628	Puerto Rico	1	DQ450028	—
Co. polygramma	—	SFC20120821-64	Korea	1	KJ609162	—
Co. polygramma	CUH:AM082	—	India	1	KJ778752	KP100303
Co. polygramma	URM 90015	—	Brazil: Amapa	1	KY074640	KY088275
Co. polygramma	URM 90016	—	Brazil: Amapa	1	KY074641	KY088274

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Co. polygramma	URM 90017	—	Brazil: Para	1	KY074642	—
Co. polygramma	MHHNU 30912	—	China	1	MK214392	—
Co. polygramma	HFJAU 0425	—	China: Jiangxi	1	MN258643	—
"Collybiopsis pseudoluxurians"						
Co. pseudoluxurians [HT]	TENN-F-068144	TFB14290	USA: Mississippi	1	KY026702; NR_137863	KJ416242
"Collybiopsis pseudomphalodes"						
"*Co. pseudomphalodes*"	NYBG REH7348	REH7348	Costa Rica	1	AF505762	—
"*Co pseudomphalodes*"	not given	PR24TN	Puerto Rico	1	AY842957	—
Collybiopsis quercophila						
Co. quercophila	TENN-F-069267	TFB14570	Slovakia	1	KY026728	KY026728
Co. quercophila	TENN-F-069320	TFB14615	USA: California	1	KY026736	KY026736
Co. quercophila	TENN-F-069321	TFB14616	USA: California	1	KY026737	KY026737
Co. quercophila	SFSU:25220	—	USA: California	1	KY026761	KY026761
Collybiopsis ramealis						
Co. ramealis	TENN-F-050324	TFB4727	Sweden	2	DQ450030	—
Co. ramealis	TENN-F-062867	TFB13520	Sweden	2	JF313670	—
Co. ramealis	TENN-F-065132	TFB13755	Belgium: Couvin	2	KJ416235	KJ189566
Co. ramealis	TENN-F-067890	TFB14140c1	Germany	2	KJ416235	KJ189566
Co. ramealis	TENN-F-065136	TFB13759	Belgium: Couvin	2	MN413344	—
Co. ramealis [ET]	TENN-F-065145	TFB13769	Belgium: Couvin	2	MN413345	MN413345
Co. ramealis	TENN-F-065146	TFB13770	Belgium: Couvin	1, 2	MN413346	MW396882
Co. ramealis	TENN-F-065147	TFB13771h1	Belgium: Couvin	2	MN413347	—
Co. ramealis	TENN-F-065147	TFB13771h2	Belgium: Couvin	2	MN413348	—
Co. ramealis	TENN-F-065151	TFB13775	Belgium: Dinante	2	MN413349	—
Co. ramealis	TENN-F-050509	TFB3772	Scotland	1, 2	MN413350	MW396885
Co. ramealis	TENN-F-067913	TFB14163h1	Germany: Thuringia	2	MN413351	—
Co. ramealis	TENN-F-067913	TFB14163h2	Germany: Thuringia	2	MN413352	—
Co. ramealis	TENN-F-067912	TFB14162h1	Germany	2	MN413353	—
Co. ramealis	TENN-F-067912	TFB14162h2	Germany	2	MN413354	—
Co. ramealis	TENN-F-067890	TFB14140c1	Germany: Thuringia	2	MN413355	—

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Co. ramealis	TENN-F-067890	TFB14140c2	Germany: Thuringia	2	MN413356	—
Co. ramealis	TENN-F-067890	TFB14140c3	Germany: Thuringia	2	MN413357	—
Co. ramealis	TENN-F-067890	TFB14140c4	Germany: Thuringia	2	MN413358	—
Co. ramealis	TENN-F-067890	TFB14140c5	Germany: Thuringia	2	MN413359	—
Co. ramealis	TENN-F-067890	TFB14140c6	Germany: Thuringia	2	MN413360	—
Co. ramealis	TENN-F-067890	TFB14140c7	Germany: Thuringia	2	MN413361	—
Co. ramealis	TENN-F-067890	TFB14140c8	Germany: Thuringia	2	MN413362	—
Co. ramealis	TENN-F-067900	TFB14150c1	Germany: Thuringia	2	MN413363	—
Co. ramealis	TENN-F-067900	TFB14150c2	Germany: Thuringia	2	MN413364	—
Co. ramealis	TENN-F-067900	TFB14150c3	Germany: Thuringia	2	MN413365	—
Co. ramealis	TENN-F-067900	TFB14150c7	Germany: Thuringia	2	MN413366	—
Co. ramealis	TENN-F-067900	TFB14150c8	Germany: Thuringia	2	MN413367	—
Co. ramealis	TENN-F-069255	TFB14559h1	Slovakia	2	MN413370	—
Co. ramealis	TENN-F-069255	TFB14559h2	Slovakia	2	MN413371	—
Co. ramealis	TENN-F-055908	TFB6989	Scotland	1, 2	MN413372	MW396883
Co. ramealis	BR 72_41	—	Belgium	1	MW396875	MW396875
Co. ramealis	TENN-F-069251	TFB14555	Slovakia	1, 2	MW405779	MW396884
Collybiopsis readiae						
Co. readiae	TENN-F-053687	TFB7571	New Zealand	1	DQ450034	—
Co. readiae	FZ1395	PDD:95844	New Zealand	1	HQ533036	—
Co. readiae	TENN-F-061061	TFB13056	New Zealand	1	KJ416244	—
Collybiopsis stenophylla						
Co. stenophylla	TENN-F-065943	TFB13998	USA: Tennessee, GSMNP	1, 2	MN413331	MW396886
Co. stenophylla	TENN-F-051099	TFB4798	USA: Georgia	1, 2	MN413330	MW396887
Co. stenophylla	TENN-F--059444	TFB11558	USA: North Carolina	2	DQ450032	—
Co. stenophylla	TENN-F--059449	TFB11559	USA: North Carolina	2	DQ450033	—
Collybiopsis subcyathiformis						
Co. subcyathiformis	URM 90023	—	Brazil: Para	1	KY404982	KY404982
Co. subcyathiformis	URM 90022	—	Brazil: Para	1	KY404983	KY404983
Collybiopsis subnuda						
Co. subnuda	TENN-F-061138	TFB12577	USA: Tennessee, GSMNP	1	KY026667	FJ750262

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Co. subnuda	WRW 08-462	—	USA: West Virginia	1	KY026765	KY026765
Co. subnuda	TENN-F-65984	TFB14043	USA: North Carolina	1	MW396876	MW396876
Collybiopsis trogioides						
C. trogioides [HT]	SFSU-AWW51	AWW51	Indonesia	1	AY263428	AY639431
"Collybiopsis utriformis"						
"*Co. utriformis*"	TENN-F-068185h1	TFB14334h1	USA: Connecticut	1	KY026707	KY026707
"*Co. utriformis*"	TENN-F-068185h2	TFB14334h2	USA: Connecticut	1	KY026708	KY026708
"*Co. utriformis*"	WRW05-1170	—	USA: West Virginia	1	KY026764	KY026764
Collybiopsis viallanti						
Co. viallanti	TENN-F-65115	TFB13739	USA: Tennessee, GSMNP	1	KY026676	KY026676
Collybiopsis villosipes						
Co. villosipes	TENN-F-056252	TFB9539	USA:	1	DQ450058	—
Co. villosipes	TENN-F-060951	TFB12836	New Zealand: Fiordland	1	KJ416255	FJ750264
Co. villosipes	iNaturalist	—	USA: California	1	MF163171	—
Collybiopsis* sp. *1						
Co. sp. 1	TENN-F-54944	TFB8605 culture	Argentina: Chubut	1	MW396870	MW396870
***Collybiopsis* sp. 2**						
Co. sp. *2*	TENN-F-051101	TFB4800	USA: Georgia	1	MW396874	MW396874
Gymnopanella nothofagi						
Gymnopanella nothofagi	SGO 163624	—	Chile	1	KT906424	KT906424
Gymnopanella nothofagi	SGO 163625	—	Chile	1	KT906425	KT906425
Gymnopus sp.						
Gymnopus VC-2017g	URM 90043	—	Brazil: Paraiba	1	KY321573	KY321573
Gymnopus VC-2017g	URM 90042	—	Brazil: Paraiba	1	KY321574	KY321574
Gymnopus VC-2017g	URM 90045	—	Brazil: Paraiba	1	KY321575	KY321575
Gymnopus sp.	environmental	olrim406	Sweden	1	KY352520	—
Gymnopus VC-2017g	URM 90054	—	Brazil: Paraiba	1	KY404984	—
Gymnopus sp.	FH: BHI-F523	BHI-F523a	USA: Maine, Peddocks Island	1	MF161290	—

Organism	Herbarium No.	Isolate	Location	Fig. no.	GenBank ITS	GenBank LSU
Mycetinis kallioneus						
My. kallioneus	GB-01505113	—	Norway: Svalbard	1	KX958397	KX958397
Mycetinis opacus						
My. opacus	TENN-F-060016	TFB11787	USA: Tennessee, GSMNP	1	KY696758	KY696758
My. opacus	TENN-F-069200	TFB14490h1	USA: Mississippi	1	KY696768	KY696768
My. opacus	TENN-F-069200	TFB14490h2	USA: Mississippi	1	KY696769	KY696769
My. opacus	TENN-F-054871	TFB9071	USA: Mississippi	1	MW396877	MW396877
My. opacus	BM071315-2	Bruce Macol 888	USA: Tennessee	1	MW396878	MW396878
Mycetinis salalis						
My. salalis	DAOM:175251	—	—	1	KX752265	KX752265
Mycetinis scorodonius						
My. scorodonius	TENN-F-050522	TFB3785	Sweden: Vastergotland	1	KY696731	KY696731
My. scorodonius	TENN-F-050689	TFB3701	USA: North Carolina	1	KY696733	KY696733
My. scorodonius	TENN-F-050696	TFB3708	USA: Tennessee, GSMNP	1	KY696734	KY696734
My. scorodonius	TENN-F-051442	TFB5031	Canada: Nova Scotia	1	KY696739	KY696739
My. scorodonius	TENN-F-053466	TFB4969	USA: New York	1	KY696741	KY696741
My. scorodonius	TENN-F-053467	TFB5025	Canada: Nova Scotia	1	KY696742	KY696742
My. scorodonius	TENN-F-053471	TFB4939	USA: New York	1	KY696746	KY696746
My. scorodonius	TENN-F-053474	TFB5005	USA: Maine	1	KY696748	KY696748
Paramycetinis austrobrevipes						
P. austrobrevipes [HT]	TENN-F-050135	TFB4033	Australia: Tasmania	1	KY026622	KY026622
P. austrobrevipes	TENN-F-053149	TFB3591	Australia: Tasmania	1	KY026637	KY026637
P. austrobrevipes	TENN-F-053181	TFB3585	Australia: Tasmania	1	KY026638	KY026638
Paramycetinis caulocystidiatus						
P. caulocystidiatus	TENN-F-053683	TFB7572	New Zealand	1	KY026642	KY026642
P. caulocystidiatus	TENN-F-053721	TFB7588	New Zealand	1	KY026643	KY026643
P. caulocystidiatus	TENN-F-053725	TFB7589	New Zealand: North Island	1	KY026644	KY026644
P. caulocystidiatus [HT]	TENN-F-054050	TFB7148	New Zealand	1	KY026645	KY026645

Materials & methods

Abbreviations: Throughout this paper, *Co* = *Collybiopsis*; *G* = *Gymnopus*; *M* = *Marasmius*; *Ma* = *Marasmiellus*. Colors cited alphanumerically are from Kornerup & Wanscher (1967) and those in quotation marks are from Ridgway (1912). BF = bright field microscopy; PhC = phase contrast microscopy (see also Petersen & Hughes 2017b). TFB = Tennessee field-book number, assigned to fresh collections in order to track specimen, photos, notes, etc.; TENN-F-XXXXXX = official designation of the herbarium of the University of Tennessee (and Mycoportal number). GSMNP = Great Smoky Mountains National Park. In basidiospore metrics, E = range of spore lengths divided by spore widths; E^m = median spore length divided by median spore width; L^m = median spore length. In descriptions L = complete lamellae; L + ll = lamellae + lamellulae Herbarium acronyms are from Index Herbariorum.

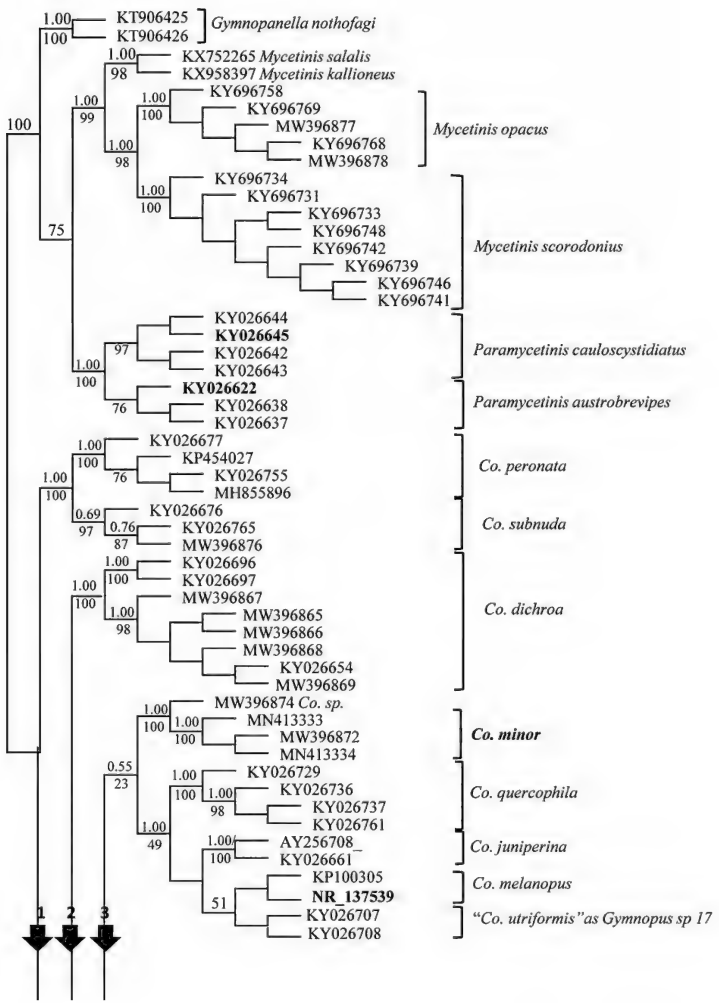
Metrics of microstructures were calculated using an Olympus BX60 microscope fitted with phase contrast imagery and photographs of microstructures were produced with an Olympus Q_c color camera. Microscope mounts were usually in 3% KOH solution or Melzer's reagent (abbr. IKI).

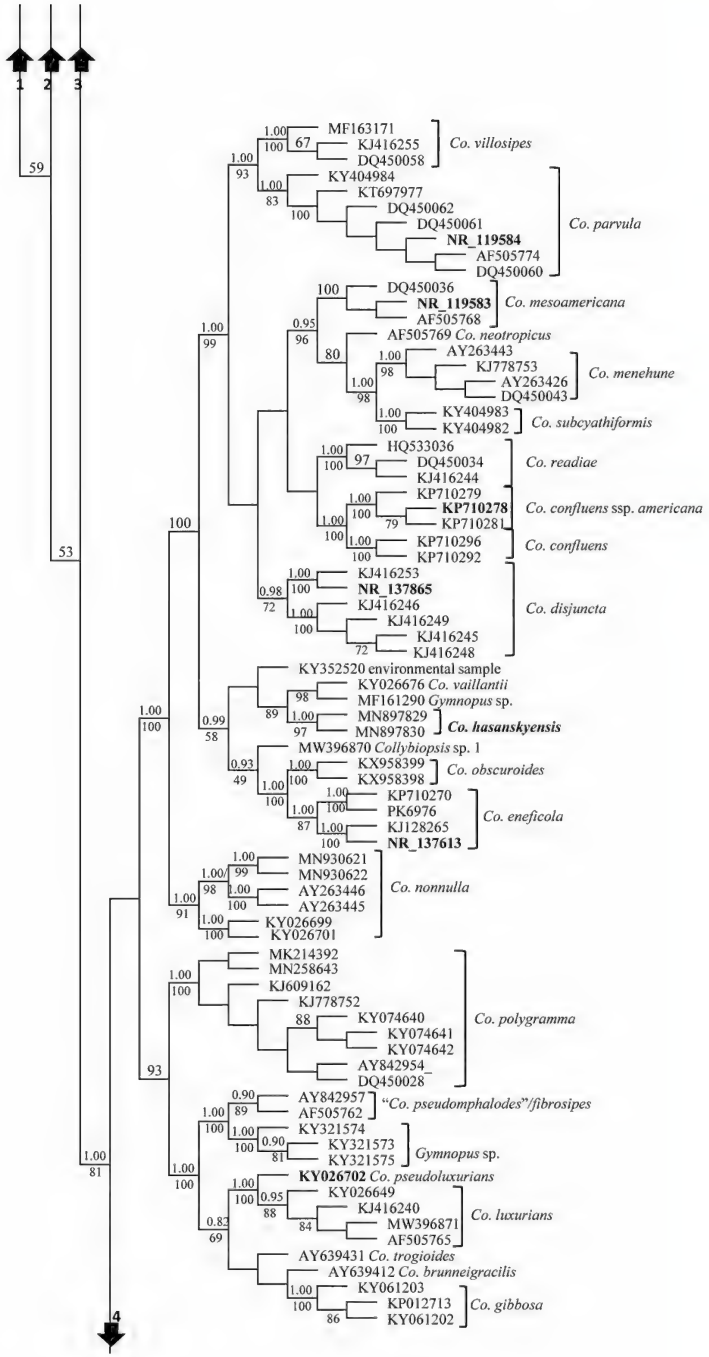
Molecular methods for DNA extractions, PCR, and Sanger sequencing of the nuclear ribosomal ITS and LSU regions were described in Aldrovandi et al. (2015). DNA sequence alignments with concatenated ITS and LSU sequences (where available (see Table 1) were performed in Geneious 11.0.3 (2017) using Clustal W (Thompson & al. 1994) then manually adjusted in AliView 1.26 (Larsson 2014). Unlike Olivera & al., (2019), we did not delete highly variable regions of the alignment because information content in these regions informed species groupings. PhyML phylogenetic analyses were performed in Geneious 11.0.3 (2017) using a Generalized Time-reversable model (GTR) with 4 nucleotide substitution rate catigories and a gamma rate variation with 4 categories. Values for the transition/transversion ratio, proportion of invariable sites, and gamma distribution parameter were estimated. 500 boot strap replications were performed. Bayesian analysis was performed in Geneious 11/0/3 using MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001) with a GTR model of evolution, 4 chains and a burn-in of 100,000. Chain length was 1,100,000. Sequences were deposited in GenBank (Table 1). Specimen data are available in Mycoportal (MyCoPortal 2018).

Taxonomy

An ITS+LSU phylogeny of *Collybiopsis* is presented in Fig. 1. *Gymnopanella nothofagi*, *Mycetinis* spp., and *Paramycetinis* spp. were selected as related outgroups based on a nrLSU phylogeny in Petersen & Hughes (2020). *Collybiopsis* as circumscribed in this paper includes *Co. dichroa*, a genetic complex of several poorly circumscribed taxa. *Collybiopsis dichroa* I and II

form natural hybrids but there is no evidence that F2 later progeny are viable (Hughes & al. 2015). *Collybiopsis ramealis* appears as sister to *Co. furtiva* and is in a larger, well-supported clade with *Co. stenophylla, Co. filamentipes, Co. californica,* and *Co. foliiphila.*




1
2
3
4
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DQ450058
Co. villosipes
KY404984
KT697977
DQ450062
DQ450061
NR_119584
AF505774
DQ450060
Co. parvula
DQ450036
NR_119583
AF505768
Co. mesoamericana
AF505769 Co. neotropicus
AY263443
KJ778753
AY263426
DQ450043
Co. menehune
KY404983
KY404982
Co. subcyathiformis
HQ533036
DQ450034
KJ416244
Co. readiae
KP710279
KP710278
KP710281
Co. confluens ssp. americana
KP710296
KP710292
Co. confluens
KJ416253
NR_137865
KJ416246
KJ416249
KJ416245
KJ416248
Co. disjuncta
KY352520 environmental sample
KY026676 Co. vaillantii
MF161290 Gymnopus sp.
MN897829
MN897830
Co. hasanskyensis
MW396870 Collybiopsis sp. 1
KX958399
KX958398
Co. obscuroides
KP710270
PK6976
KJ128265
NR_137613
Co. eneficola
MN930621
MN930622
AY263446
AY263445
KY026699
KY026701
Co. nonnulla
MK214392
MN258643
KJ609162
KJ778752
KY074640
KY074641
KY074642
AY842954
DQ450028
Co. polygramma
AY842957
AF505762
"Co. pseudomphalodes"/fibrosipes
KY321574
KY321573
KY321575
Gymnopus sp.
KY026702 Co. pseudoluxurians
KY026649
KJ416240
MW396871
AF505765
Co. luxurians
AY639431 Co. trogioides
AY639412 Co. brunneigracilis
KY061203
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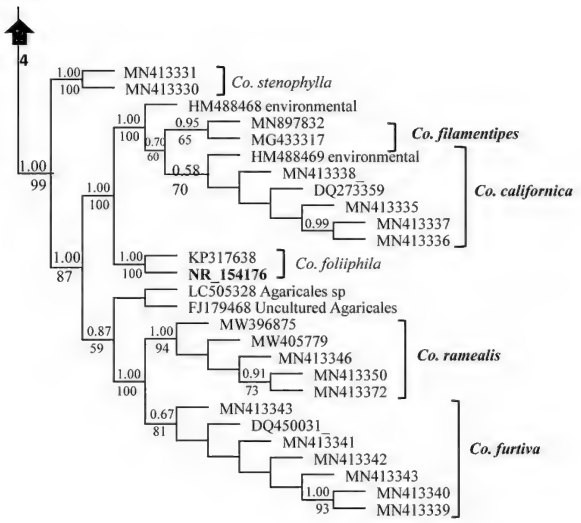
KY061202
Co. gibbosa



Figs 1A, B, C. PhyML tree of concatenated nrITS and LSU *Collybiopsis* sequences. Support values at the nodes consist of Bayesian posterior probabilities (top value) and PhyML bootstrap support based on 500 replications (bottom value). The outgroup comprises *Gymnopanella* and *Mycetinis*. The label on each branch represents the nrITS GenBank accession number. Corresponding LSU sequences are given in Table 1. GenBank accession numbers in bold represent types. Taxa described in this paper are also in bold. The phylogeny is divided into three parts with arrows connecting each part.

An nrITS-based phylogeny including all sequenced collections of *Co. ramealis* (Fig. 2) demonstrates that *Co. ramealis* represents a complex, not a single taxon. Several issues are resolved or raised. First, European collections are very nearly homogeneous based on nrITS sequences, so topotype *Co. ramealis* remains a circumscribable taxon well described by Antonín & Noordeloos (2010) and below. Examination of nrITS sequences reveals, however, that the European population consists of two ITS haplotypes and hybrids, with indications that genetic recombination has occurred between haplotypes. Conversely, at least some North American collections (to this time limited to southeastern North America), are clearly separated from *Co. ramealis,* and are here described as *Co. furtiva*. Likewise, *Marasmiellus ramealis* var. *californicus* lies within *Collybiopsis*, discrete at species rank and more widely distributed than anticipated.

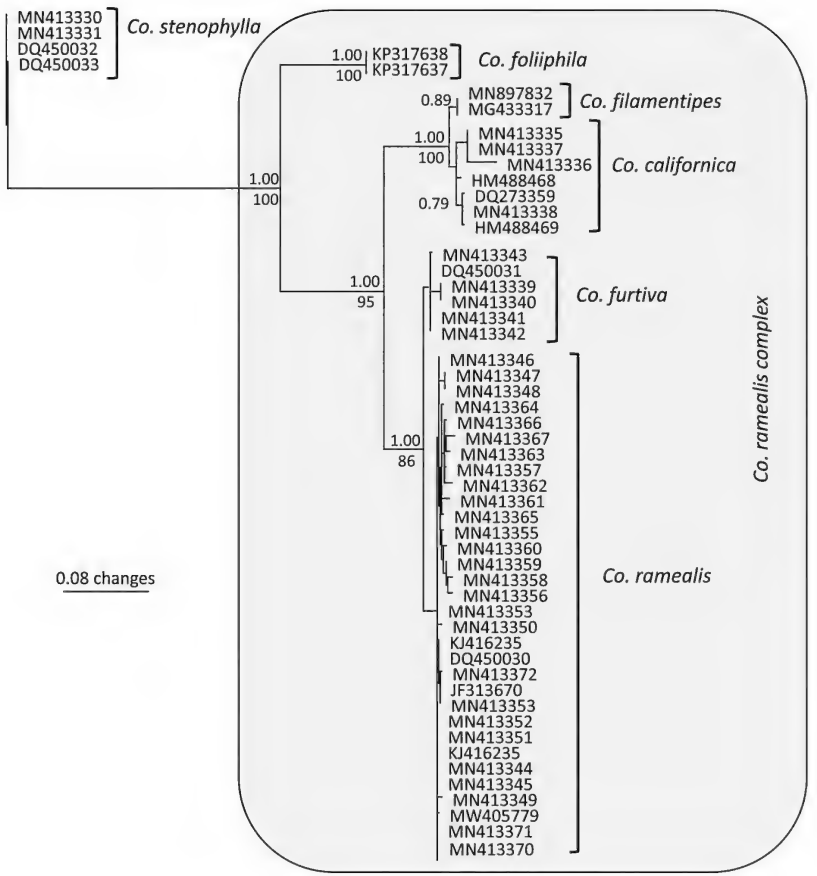


FIG. 2. PhyML tree of nrITS sequences representing the *Collybiopsis ramealis* complex. *Collybiopsis stenophylla* was used as an outgroup. Support values at the nodes consist of Bayesian posterior probabilities (top value) and PhyML bootstrap support based on 500 replications (bottom value). The label on each branch represents the nrITS GenBank accession number.

Taxonomic analyses

Collybiopsis californica (Desjardin) R.H. Petersen, **stat. nov.** FIGS 3–13

IF 556204

BASIONYM: *Marasmiellus ramealis* var. *californicus* Desjardin, Mycologia 79: 132. 1987.

HOLOTYPE: USA, California, Los Angeles Co., San Dimas, 34°06′23″N 117°48′25″W, 9.III.1983, Wright 2941 (SFSU-F s.n.).

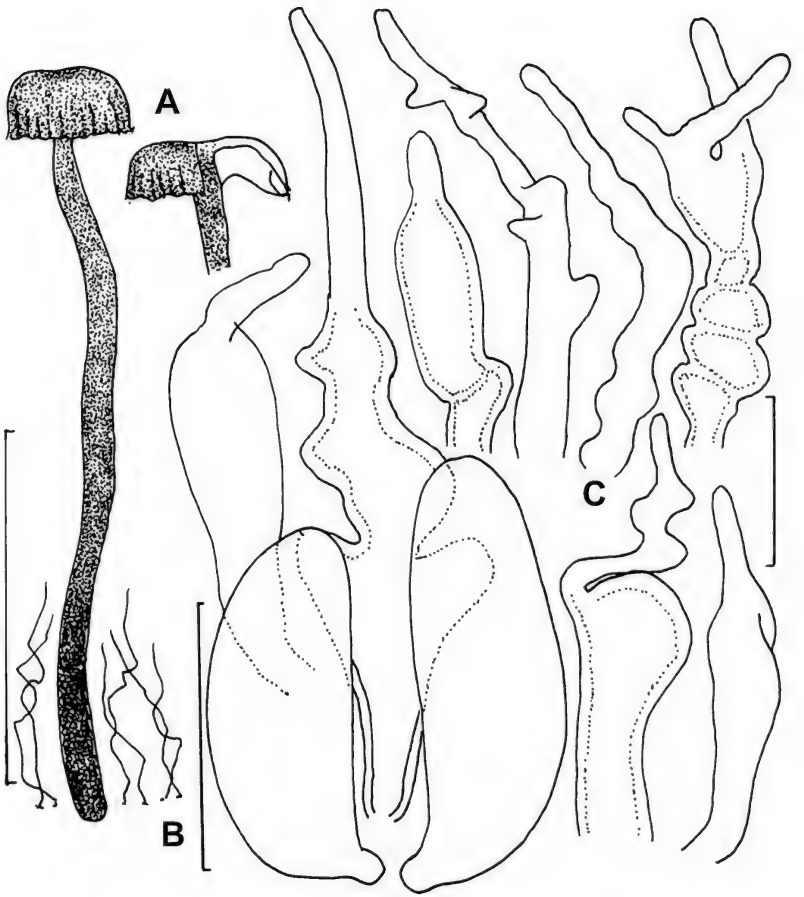


Fig. 3. *Collybiopsis californica* (Wright 866; SFSU–F-024539).
A. Basidiomata and rhizomorphs. B. Basidiospores. C. Termini of caulocystidia.
Scale bars: A = 10 mm; B = 5 µm; C = 10 µm.

Desjardin (1987) offered a detailed, comprehensive description of *Marasmiellus ramealis* var. *californicus*. Our Fig. 2 indicates that the taxon, while related to *Co. ramealis* (both European and putative American), is separable from *Co. ramealis* at species rank, triggering the rank change above. The following items are worthy of note: 1) photographic images and discussion of microstructures (Figs 3–13); and 2) the taxon's apparent extended geographic distribution.

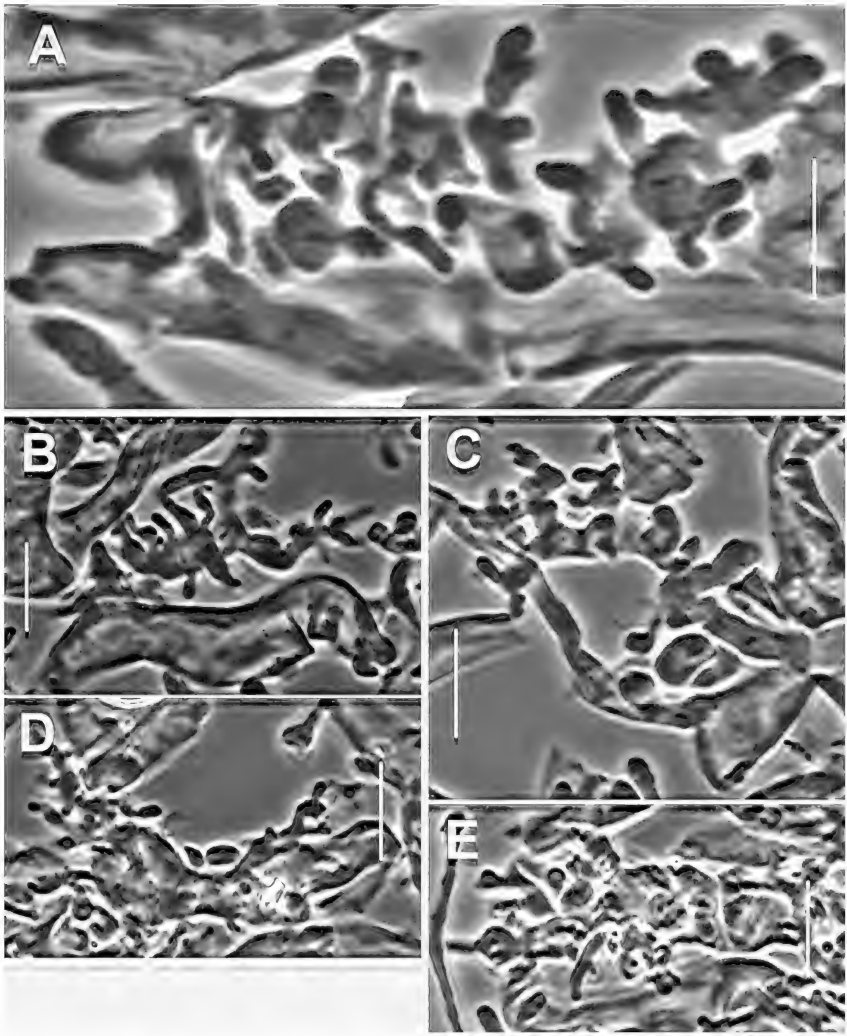


Fig. 4. *Collybiopsis californica*. (Wright 2941 SFSU s.n.).
Diverticulate pileipellis hyphae. Scale bars = 10 µm.

A comparison of microstructures of *Co. californica* (Figs 3–13) with those of *Co. ramealis* (Figs 50–60) includes the nature of the structure of pileipellis hyphae. In *Co. ramealis*, diverticula are slender, digitate and appear rigid, while those of *Co. californica* (Fig. 5) are broad, often fin- or node-like, gnarled and repeatedly branched. Pleurocystidia (Fig. 6), basidioles, and basidia (Fig. 7)

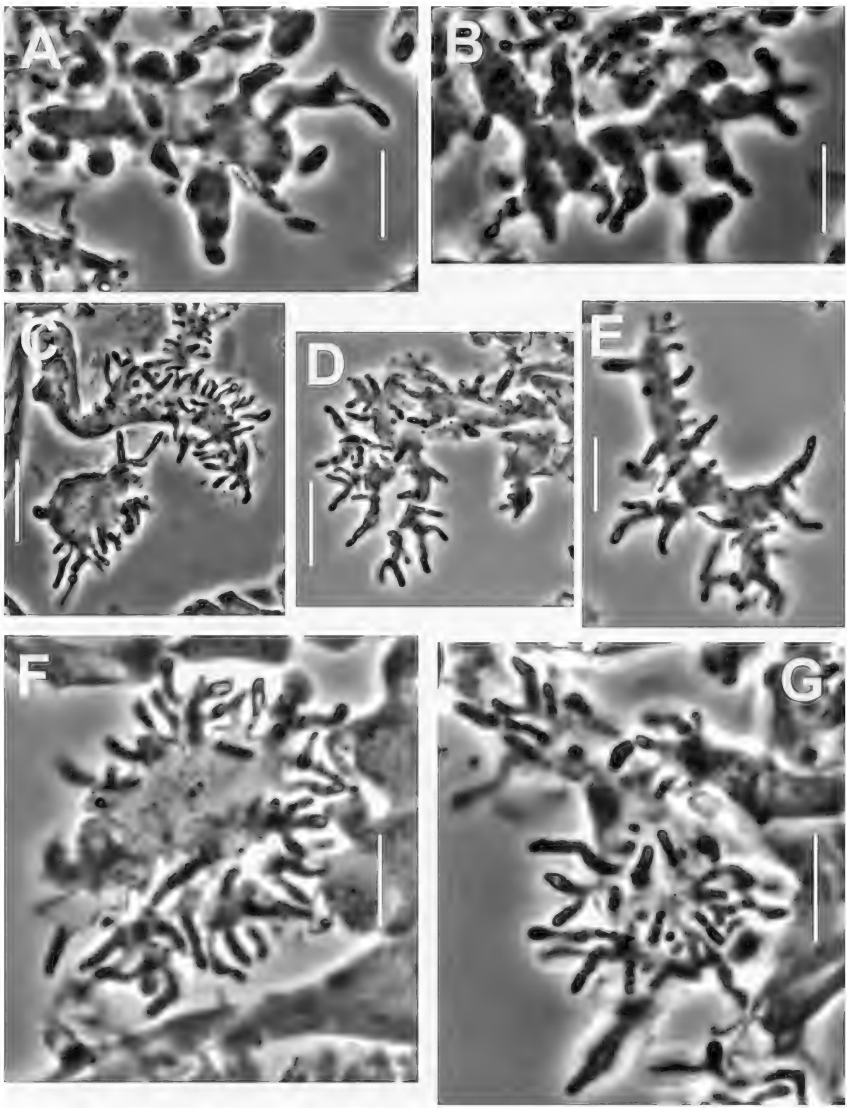


Fig. 5. *Collybiopsis californica*. (TFB 5787; TENN-F-052617). Pileipellis elements. A, B. Lobate-diverticulate elements. C-G. Diverticulate elements.

are similar to those of *Co. ramealis*, although somewhat longer. The variability of cheilocystidial shape from broadly clavate to ventricose-rostrate (Figs 8–11) is notable, but lengths and breadths of diverticula (which are often

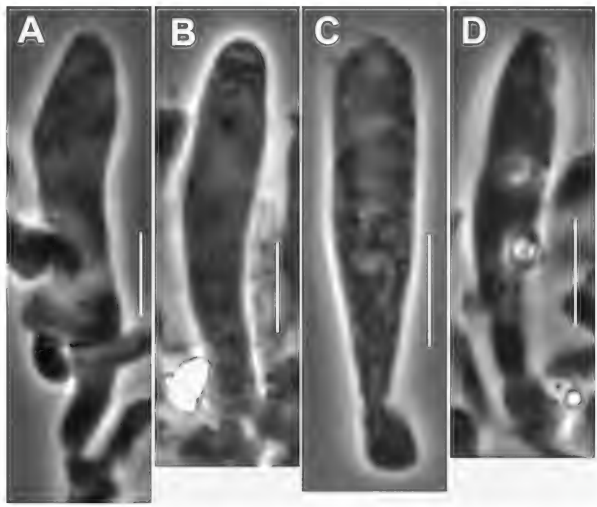


FIG. 6. *Collybiopsis californica*. (Wright 866; SFSU–F-024539). Pleurocystidia. Scale bars = 10 µm.

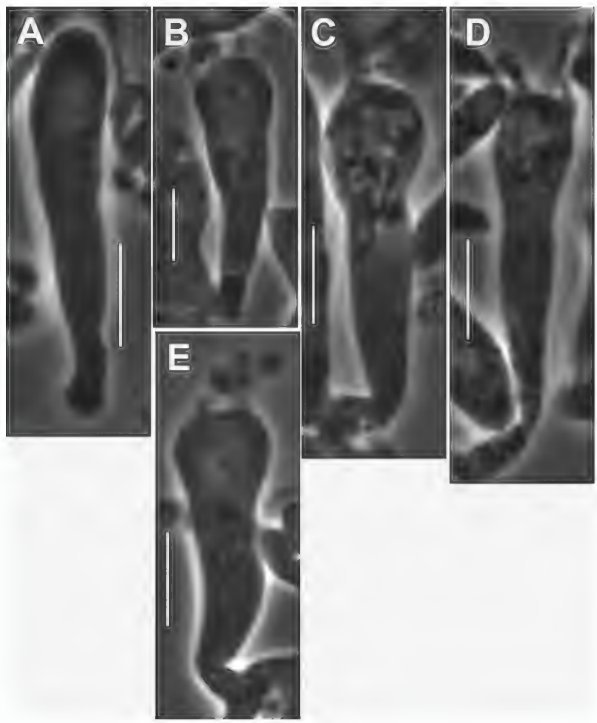


FIG. 7. *Collybiopsis californica* (Wright 2941; SFSU s.n.).
A. Basidiole. B-E. Basidia. Scale bars = 10 µm.

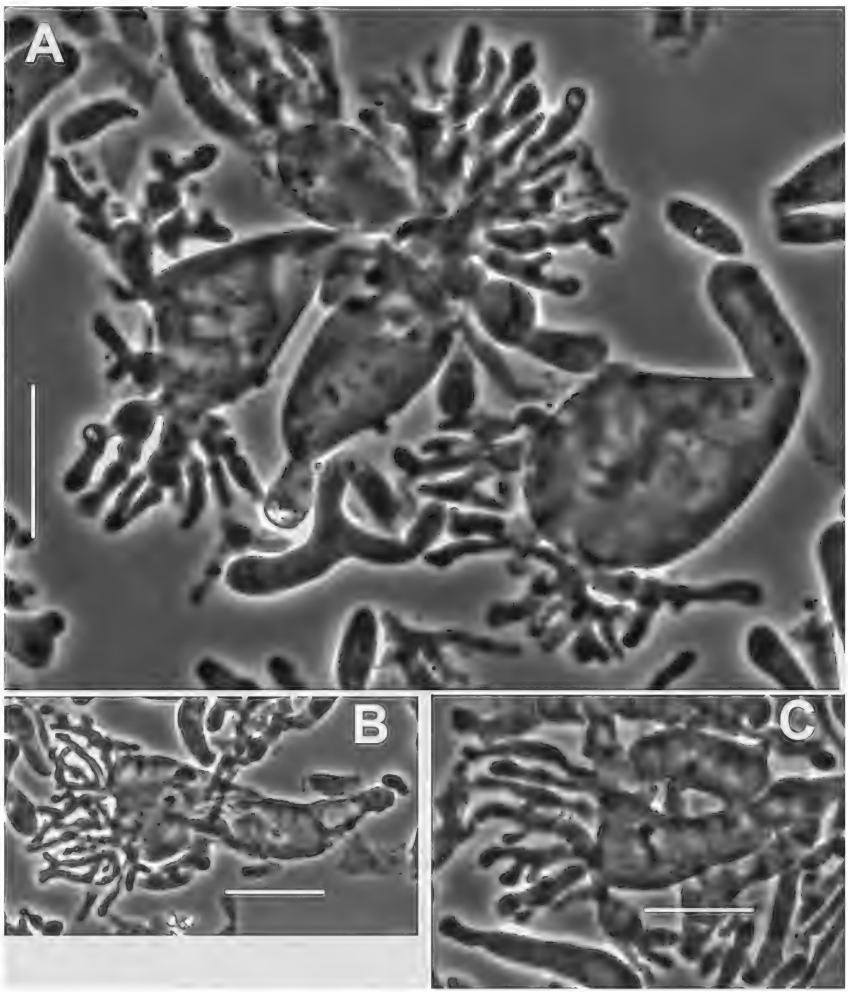


Fig. 8. *Collybiopsis californica*. (Wright 2941; SFSU s.n.). Cheilocystidia.
A. Cluster of three individuals. B, C. Individual cheilocystidia. Scale bars = 10 µm.

subcapitate) are much longer and stouter. More intriguing, cheilocystidia of *Co. californica* are often transversely septate (apparently non-clamped; Figs. 11) and apparently easily disarticulated at this septum. The result is frequent subglobose to ventricose diverticulate structures with no evidence of stalk. Whether these structures could act as propagules is unknown. Finally, caulocystidia predictably range from short, simple, individual lobes at upper stipe (Figs 12, 13) to mid- or lower stipe vesture comprising

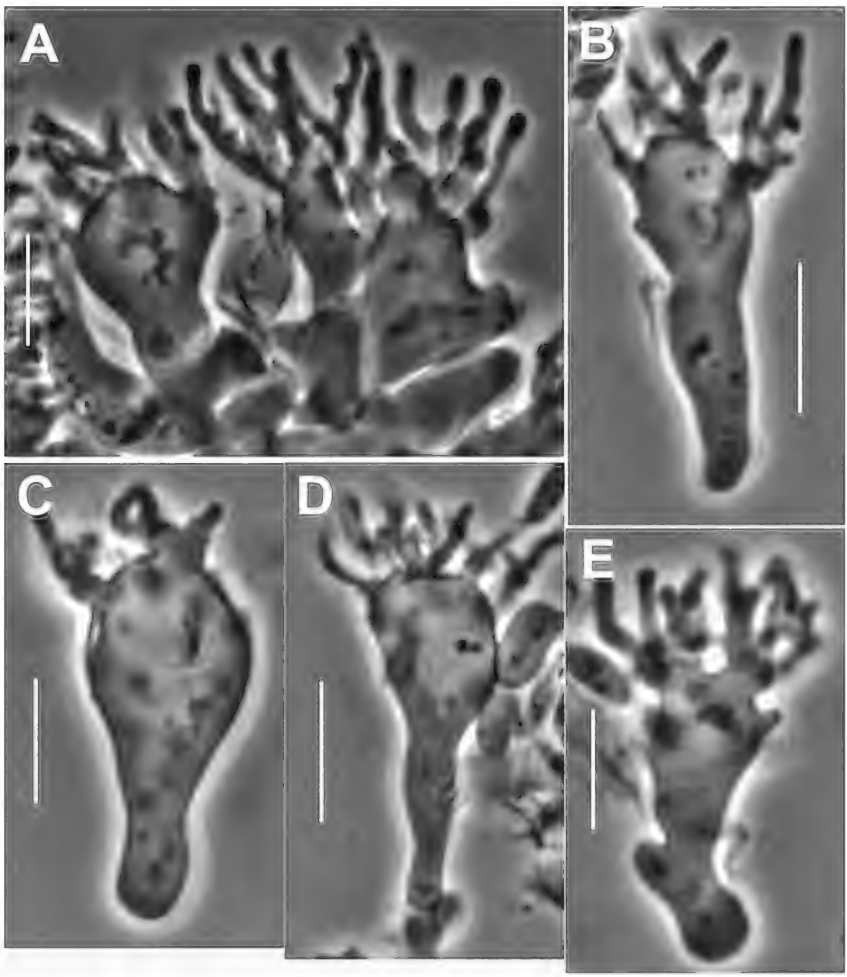


Fig. 9. *Collybiopsis californica.* (DED 8372; SFSU-F-024526). Cheilocystidia. A. Cluster of three individuals. B-E. Individual cheilocystidia.

fascicles of hyphae perpendicular to stipe surface. Smaller such fascicles (Fig. I3) are synnematoid while larger assemblages are acervuloid.

At the time of initial proposal, all collections of *Co. californica* had been gathered in southern California. Since then, samples of mycelial mats under *Pseudotsuga menziesii* in northern California and roots of *Lithocarpus densiflorus* in Oregon have yielded sequences quite similar to those of the southern Californian collections (Bergemann & Garbelotto

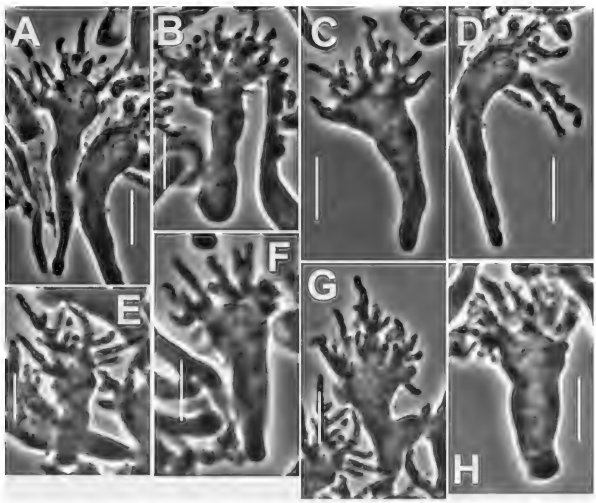


Fig. 10. *Collybiopsis californica*. (TFB 5787; TENN-F-052617). Cheilocystidia. Scale bars = 10 µm.

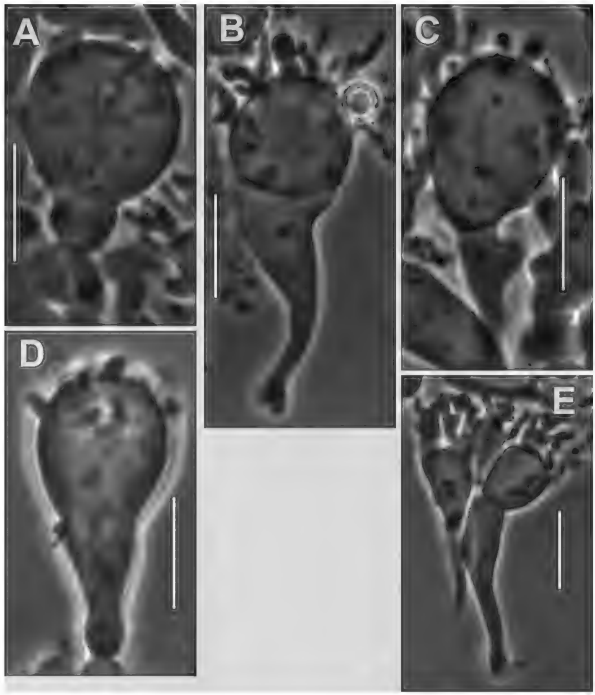


Fig. 11. *Collybiopsis californica*. (DED 8372; SFSU-F-024526). Cheilocystidia. A. Constricted by not septate cheilocystidium. B, C, E. Septate cheilocystidia. D. Cheilocystidium with septum below constriction. Scale bars = 10 µm.

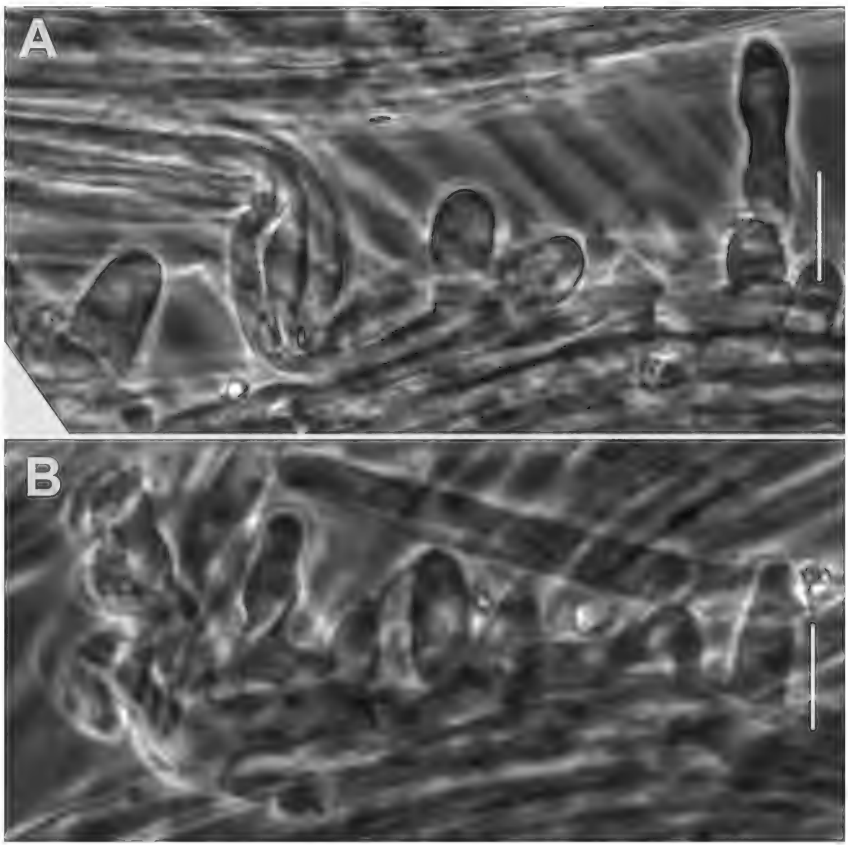


Fig. 12. *Collybiopsis californica*. (DED 8372; SFSU-F-024526). Upper stipe ornamentation; individual nodose, digitate caulocystidia. Scale bars = 10 µm.

2006; Kluber & al. 2011). Likewise, a sequence from a British Columbian collection (Canada, TENN-F-052617) matches the Californian collections. The species, obviously, exhibits a much wider distribution than originally conceived.

Pileipellis hyphal morphology is reminiscent of that of *Gymnopus pyracanthoides* (Petersen & Hughes 2016), especially regarding the complexity of diverticulate hyphae and broom cell-like termini of pileipellis hyphae. Basidiomata of the latter species, however, exhibit a slime matrix in the stipe medulla and the pileipellis includes some scanty evidence of gelatinous matrix, placing it in *Gymnopus* sect. *Perforantes*.

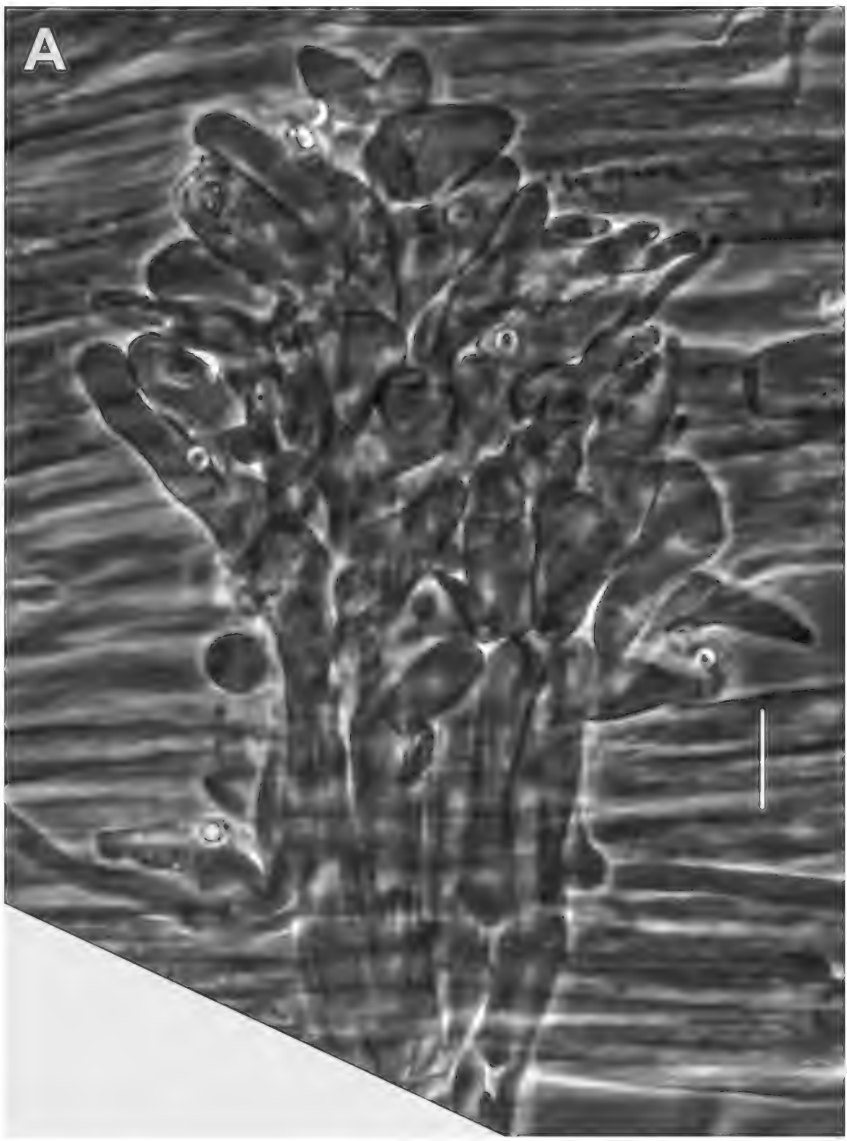


Fig. 13. *Collybiopsis californica*. (DED 8372; SFSU-F-0024526). Mid-stipe ornamentation. Synnematoid fascicle of caulocystidia. Scale bar = 10 μm.

Additional specimens examined: **CANADA**, **British Columbia**, Chilliwack River Valley, 49°09′38″N 121°57′02″W, 8.X.1992, coll. RHP (as *Marasmius androsaceus*), TFB 5787 (TENN-F-052617). **USA**, **California**, **Los Angeles Co.**, Marshall Canyon, 34°06′23″N 117°48′25″W, 12.I.1978, coll. G Wright, det. DE Desjardin, Wright 866 (SFSU-F-024539); **Marin Co.**, Point Reyes Nat. Seashore, Horse Trail, 38.043191 N, 122.802687, Wright 2941 (SASFU s.n.); , W, 11.XI.2008, coll. & det. DE Desjardin, DED 8372 (SFSU-F-024526); **Trinity Co.**, Rte 299. Grey's Falls Campground,40°51′26″N 123°29′30″W, 15.XI.1999. coll. D Largent, TFB 8088 (TENJN-F-055412).

Collybiopsis filamentipes R.H. Petersen, **sp. nov.** Figs. 14-23

IF 557073

Differs from *Co. furtiva* in its narrower basidiospores, its caulocystidial shape and distribution, and its longer and thinner stipe.

Type: USA, Tennessee, Knox Co., Knoxville, 3613 Timberlake Dr., 35°54′49″N 83°57′58″W, 22.VIII.2011, coll. RHP, TFB 13962 (**Holotype**, TENN-F-065861).

Etymology: Referring to the long, slender stipe.

Basidiomata (Fig. 14A, 15) diminutive, gracile, decidedly mycenoid. Pileus 2–11 mm broad, strongly convex when young, later shallowly convex, matt; disc near "pinkish buff" 6A3, outward somewhat paler, hardly changing color upon drying. Lamellae adnexed to subdecurrent, few (L + ll = 12–13; L = 0–1), thickish with rounded edge with no anastomoses or buttressing, subventricose, off-white, developing pastel cantaloupe necropigment upon drying. Stipe 12–21 × 0.5–1 mm, concolorous with lamellae above, slightly darker downward but never darker than "sayal brown" 6C5 developing cantaloupe colored necropigment upon drying, not insititious, upward sometimes subsaccharine, downward almost glabrous. Taste and odor negligible. Rhizomorphs absent.

Habitat & distribution: apparently associated with *Poaceae* (lawn grass, dead fine roots of ornamental bamboo); so far extremely restricted to a small area of eastern Tennessee; mid-summer. Known only from the type locality with two collections (1970, 2011).

Pileipellis constructed of three elements with intermediate forms: 1) repent, inflated, free-form hyphae <14 µm diam, firm-walled, inconspicuously clamped (due to hyphal inflation), barely roughened to distinctly encrusted in small, densely gregarious patches – no annular or helical patterns observed, with frequent secondary septa (cloissons de retret) (Figs.16, 17); 2) repent hyphae as in 1) but beset with diverticulate to setuloid ornamentation (Fig.18C); setulae <6 × 1–1.5 µm; diverticula <9 × 1–2.5 µm at base, lobate to conical, simple to variously branched;

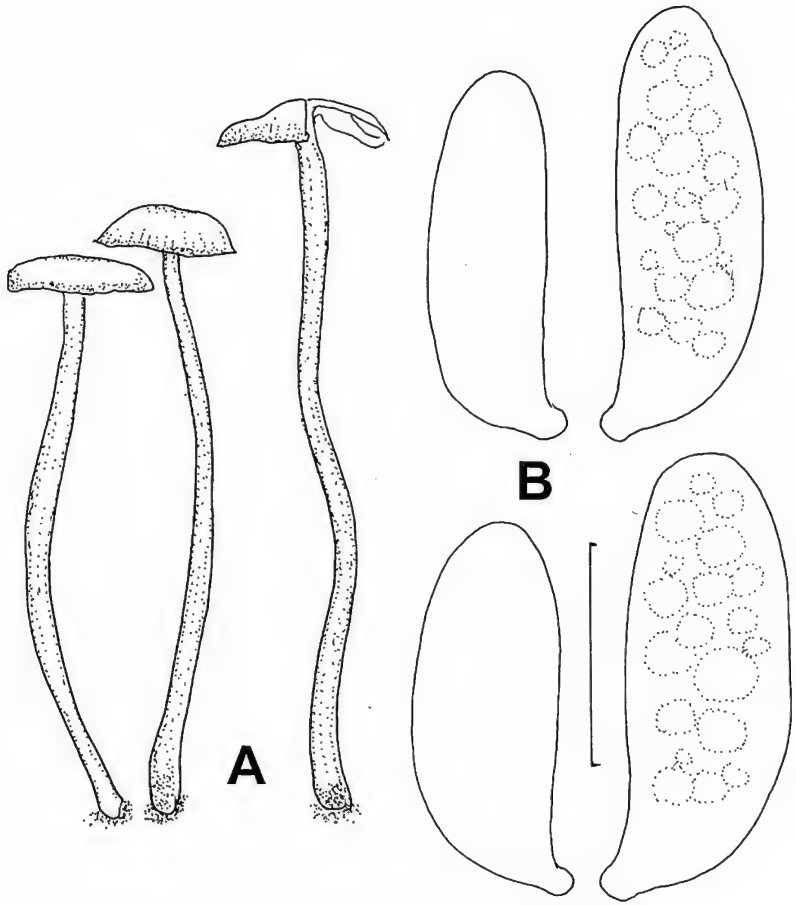


Fig. 14. *Collybiopsis filamentipes*. A. Basidiomata. (TFB 13962; TENN-F-065861). B. Basidiospores (upper = TFB 13962; lower = LRH 35861). Scale bar = 5 µm (for spores); 5 mm (for basidiomata).

and 3) hyphal termini (Fig 18A, B, D) as in 2), usually antler-branched and with setulae and/or diverticula. Pileus and lamellar trama interwoven; hyphae 3–13 µm diam, thin- to firm-walled, conspicuously clamped. Pleurocystidia (Fig. 19) 25–32 × 6–8 µm, stalked-fusiform, rounded apically, inconspicuously clamped; contents multigranular or multiguttulate,

Fig. 15. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Basidiomata (dried). Scale bar = 10 mm.

occasionally partitioned. Basidia 26–33 × 7–8 µm, clavate, 4-sterigmate, inconspicuously clamped; contents multiguttulate, usually with one major distal guttule. Basidiospores (Fig. 14B) 8–9.5(–10.5) × 2.5–3.5 µm (E = 2.29–3.80; E^m = 2.96; L^m = 8.8 µm), cylindrical to elongate-ellipsoid, thin-walled, smooth, inamyloid; contents multiguttulate, the guttules usually bipolar. Lamellar edge composed of two elements: 1) cheilocystidia (Figs. 20, 21A–C) plentiful, typically clavate to broadly clavate, 35–70 × 8–18(–25) µm, occasionally stoutly dichotomous, conspicuously clamped, hyaline, firm-walled, surmounted by numerous diverticula; diverticula 3–15 × 1.5–2 µm, appearing flexuous (not rigid), often branched, sometimes repeatedly so; and 2) diverticulate hyphae (Fig. 21D, E, 22) 5–8 µm diam, firm-walled with diverticula in files; diverticula as in 1) above. Stipe medullary hyphae (2–)3.5–7.5 diam, hyaline, embedded in a slime matrix, strictly parallel, thick-walled (wall <1.5 µm thick, hyaline), inconspicuously clamped. Stipe cortical hyphae 2–6.5 µm diam, thick-walled (wall 1.5 µm thick, golden ochre), inconspicuously clamped, producing hyphal termini and side branches (caulocystidia) perpendicular to stipe surface.

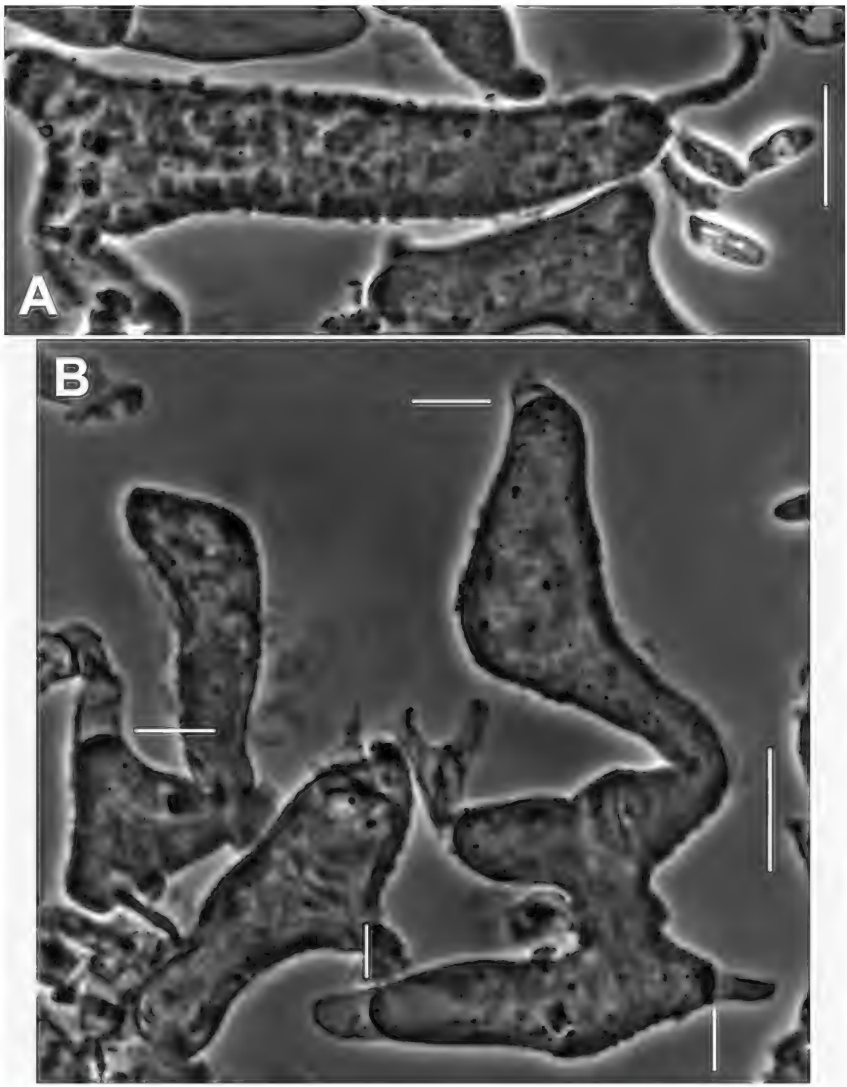


Fig. 16. *Collybiopsis filamentipes.* (TFB 13962; TENN-F-065861). Pileipellis.
A. Intricately encrusted hypha with apical diverticulate outgrowth. Note basidiospores.
B. Free-form hyphae. Short lines indicate secondary septa.
Scale bars = 10 µm.

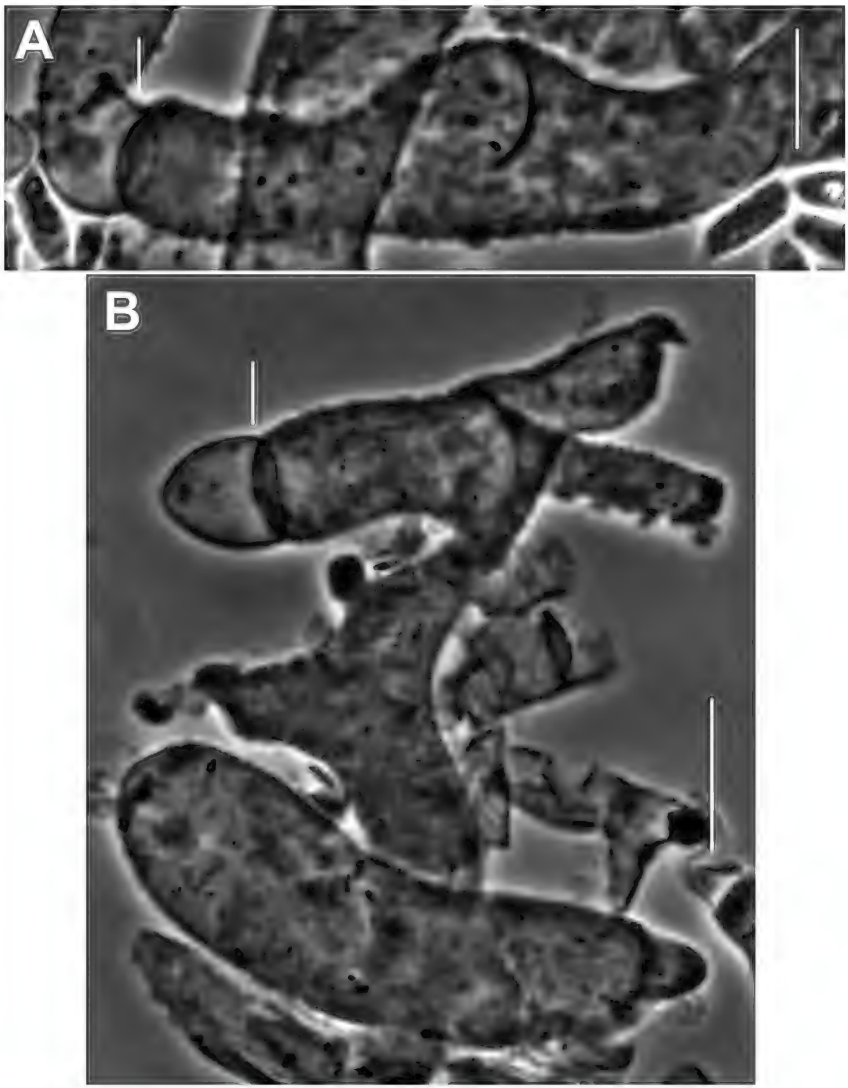


Fig. 17. *Collybiopsis filamentipes.* (TFB 13962; TENN-F-065861). Pileipellis.
Inflated, repent hyphae with moderate encrustation.
Short lines indicate secondary septa.
Scale bars = 10 μm.

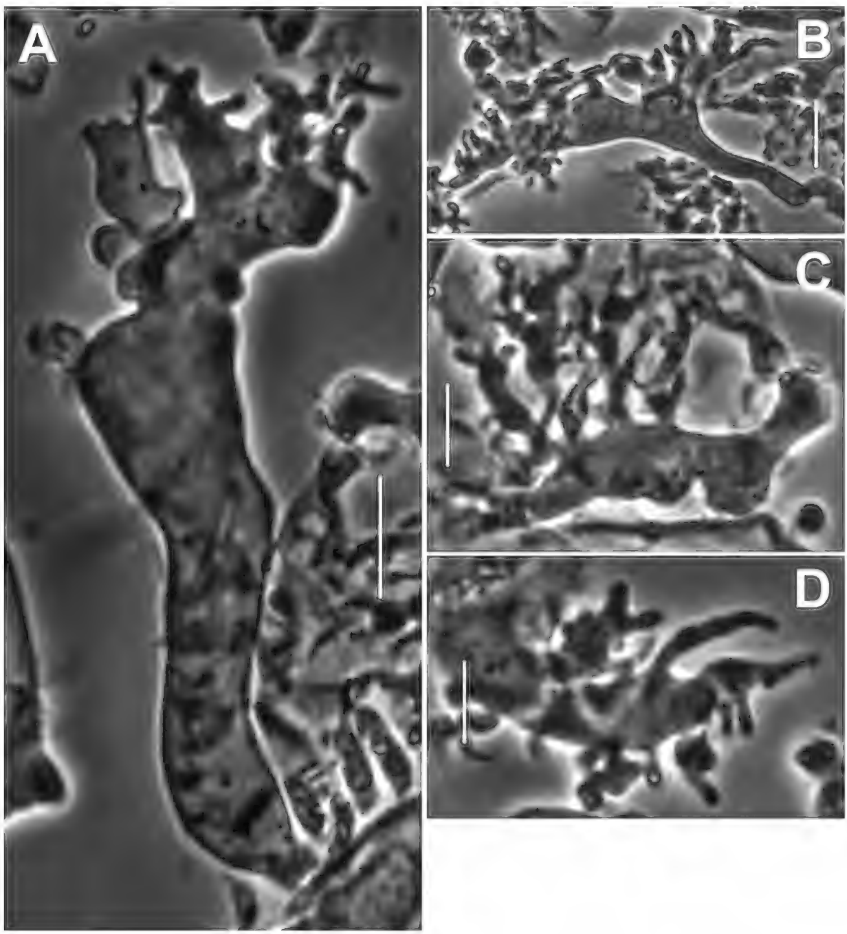


Fig. 18. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Pileipellis. Diverticulate hyphae. A. Inflated hypha with apical diverticula. B, D. Hyphal terminus with diverticula. C. Diverticulate hypha. Scale bars = 10 µm.

Caulocystidia (Fig. 23) 5–20(–40) × 6–9 µm, columnar to digitate, rarely branched, firm-walled, hyaline, without clamp connections, detersile.

Commentary: Basidiomata of *Co. filamentipes* resemble those of *Co. furtiva*, a southeastern American species in the *Co. ramealis* complex. An even closer molecular match (~99%) is with *Co. californica*, distributed along the

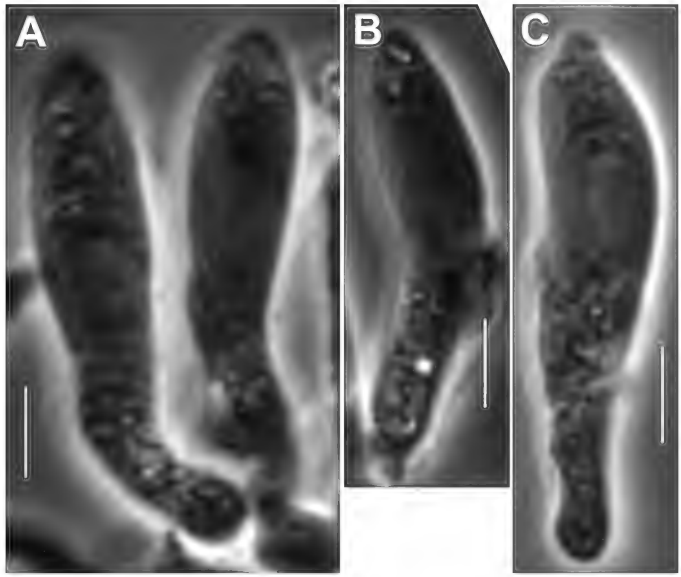


Fig. 19. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Pleurocystidia. Scale bars = 10 µm.

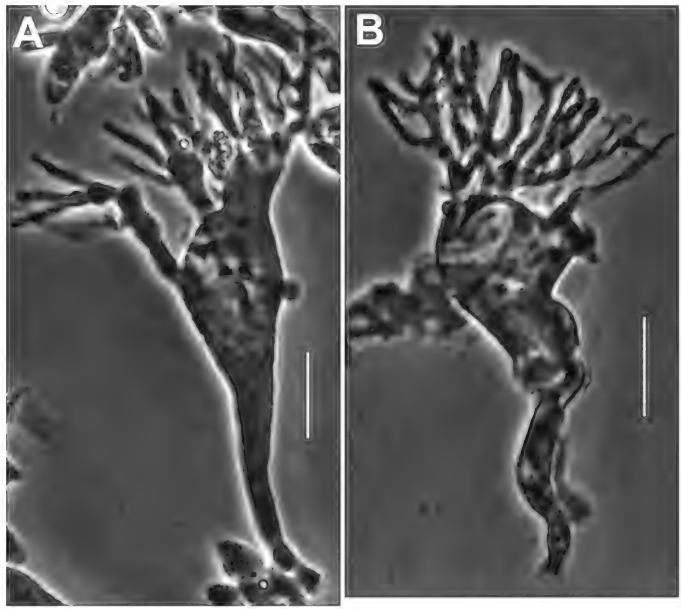


Fig. 20. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Cheilocystidia. Scale bars = 10 µm.

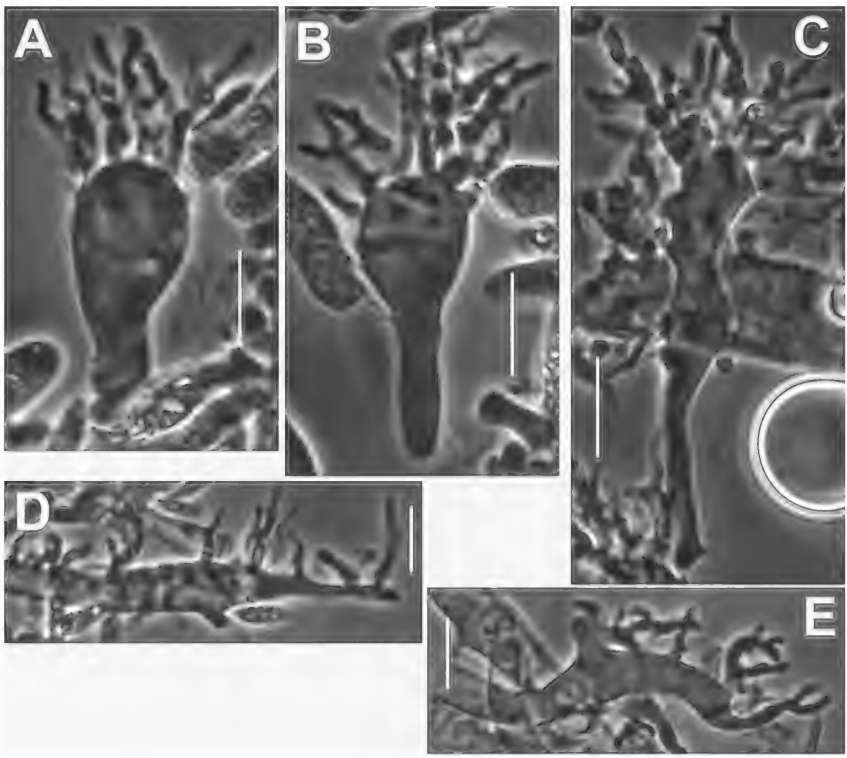


Fig. 21. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Cheilocystidia.
A-C. Typical forms with apical diverticula.
D, E. Diverticulate hyphae of the hymenium.
Scale bars = 10 µm.

North American west coast. *Collybiopsis filamentipes* shares with both inflated cells in the pileipellis, *Rameales*-structure pileipellis, cheilocystidia bearing long tentacular diverticula, spore shape (*Co. furtiva* spores slightly wider than those of *Co. filamentipes*) and caulocystidia shape and distribution. Basidiomatal stature is surely different; stipe (and therefore the stipe length to pileus breadth ratio) is much longer and thinner in *Co. filamentipes* than in *Co. furtiva* and *Co. californica.*

Collybiopsis filamentipes adds to the *Co. ramealis* clade, species of which exhibit small micromorphological differences separable only with molecular techniques and/or a careful and practiced eye. As in other such compact clades, geographical distributions seem to support micromorphological

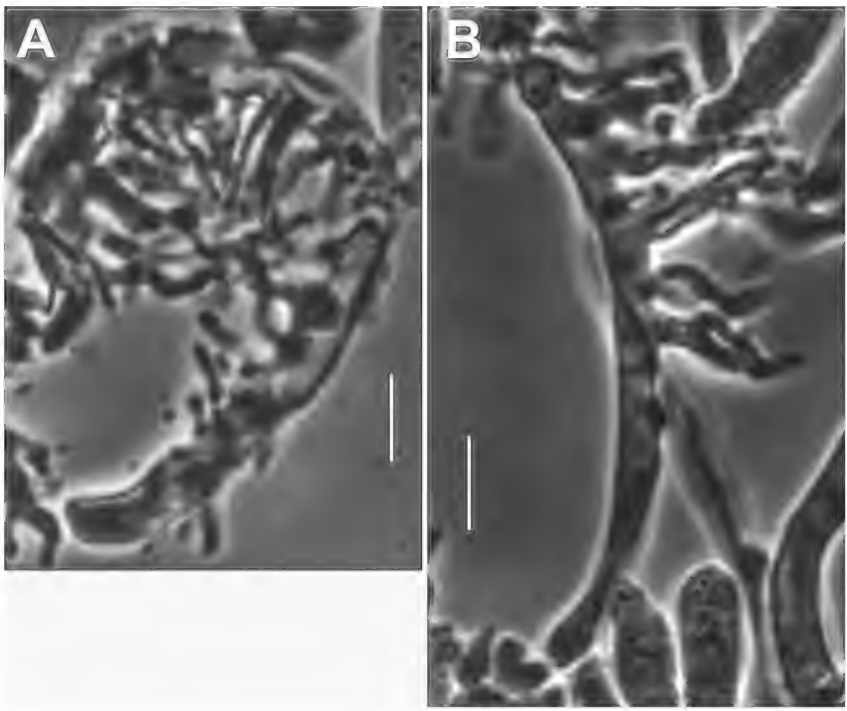


Fig. 22. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Diverticulate hyphae of the hymenium. Scale bars = 10 μm.

and molecular evidence. That *Co. ramealis* seems not to occur in North America, and seems replaced by *Co. californica, Co. filamentipes* and *Co. furtiva* reflects the same situation in other agaric groups [e.g., *Megacollybia rodmanii* for *M. platyphylla* (Hughes & al. 2008); *Collybiopsis confluens* subsp. *campanulatus* in North America for the type subspecies in Europe (Hughes & Petersen 2015); *Sparassis americana* for *S. crispa* (Hughes & al. (2014, 2015)].

Interestingly, some years after collection of the holotype specimen in 2011, the Hesler specimen was discovered in the herbarium under "*Marasmiellus* sp.," collected some 40 years previously within 100 m from the topotype location.

Additional specimen examined: **USA, Tennessee, Knox Co.**, Knoxville, Timberlake Dr., Hesler's house, 1.VIII.1970, coll. LR Hesler, LRH 35861 (TENN-F-035861).

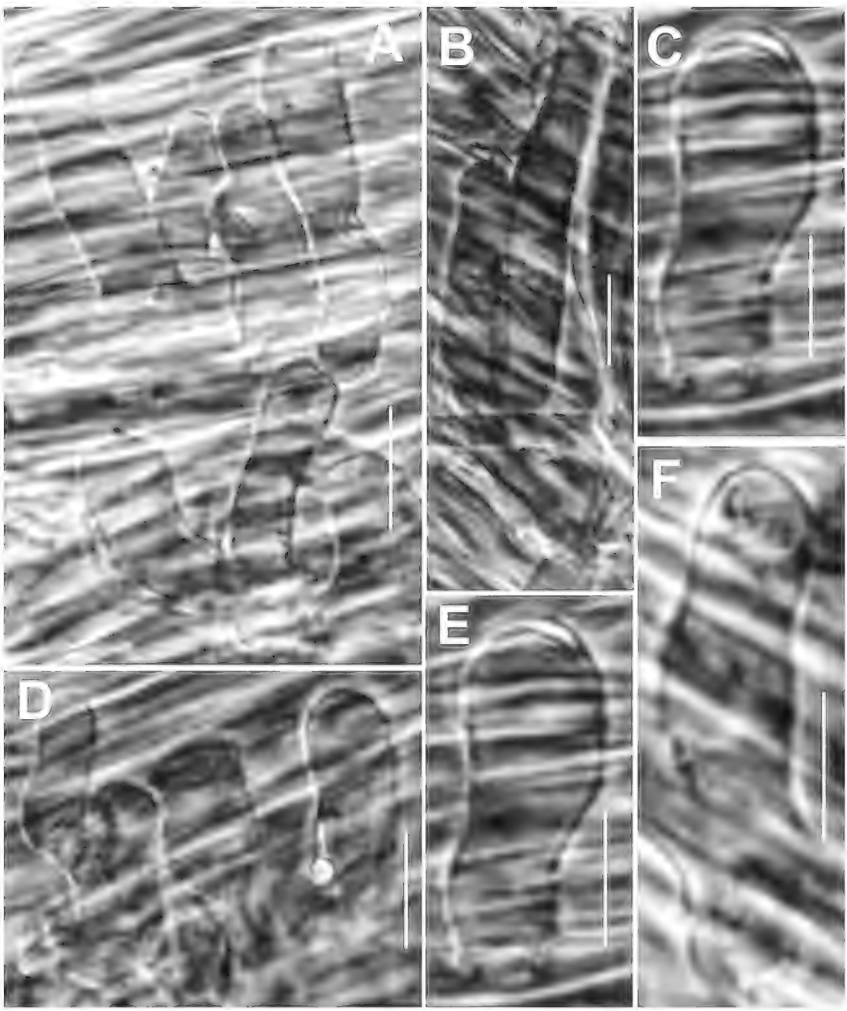


Fig. 23. *Collybiopsis filamentipes*. (TFB 13962; TENN-F-065861). Caulocystidia. A, B, D. Clusters of Caulocystidia. C, E, F. Individual caulocystidia. Scale bars = 10 µm.

Collybiopsis furtiva R.H. Petersen, **sp. nov.** FIGS. 24-34

IF 556208

Differs from Old World *Co. ramealis* by its distinct molecular profile; its hyaline (not pigmented) cheilocystidia; and its generally smaller basidiomata.

TYPE: USA, North Carolina, Macon Co., vic. Highlands, Horse Cove, Rustic Falls area, 35°02′17″N 83°09′32″W, 10.VIII.1987, coll. DE Desjardin (as *Ma. ramealis*), DED 4425 (**Holotype**, SSFU-F-024540).

ETYMOLOGY: *furtiva* = furtive, underhanded, secretive, referring to prior identification as *Co. ramealis.*

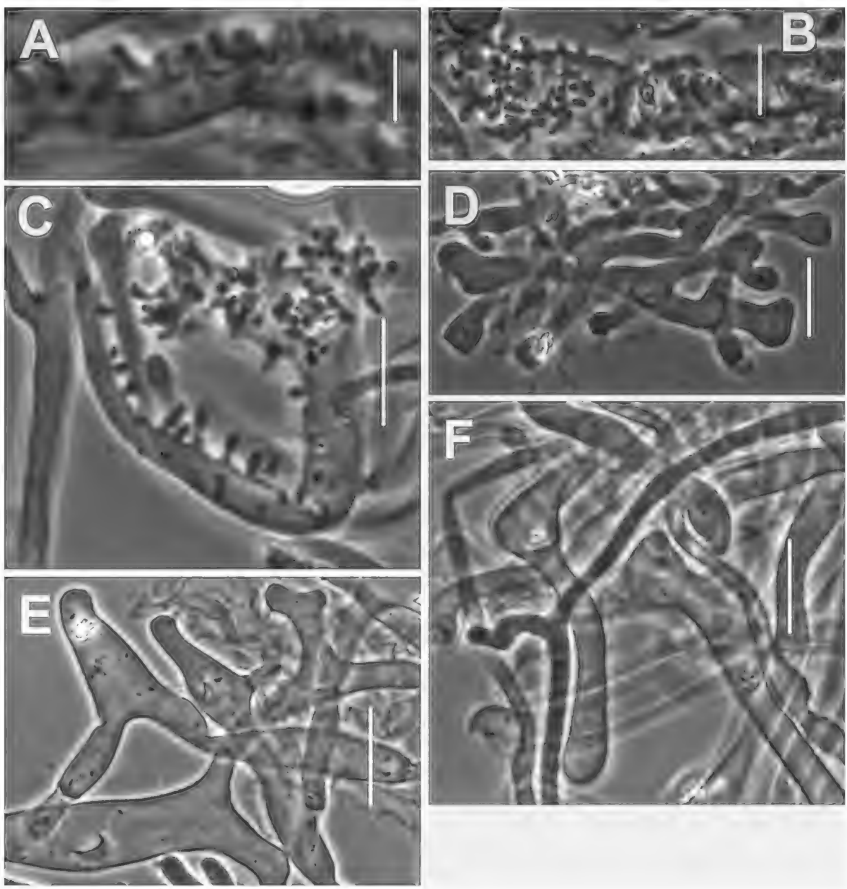


FIG. 24. *Collybiopsis furtiva.* (TFB 11558; TENN-F-059444). Pileipellis and pileus trama. A, B. Diverticulate hyphae of pileus surface. C. Diverticulate hypha ending in a "broom cell-like" hyphal terminus. D. "Antler-shaped" hyphae of subpellis. E. Swollen cells of pileus trama. F. Slender hypha among swollen hyphae of pileus trama. Scale bars = 10 μm.

Basidiomata diminutive, ratio of stipe length to pileus diameter low. Pileus 5–12 mm broad, strongly convex to subglobose when young, expanding to become shallowly convex to plano-convex with involute margin, finally applanate with upturned margin, opaque, consistently sulcate-striate near margin, matt; disc unicolorous or tinged brownish to avellaneous, otherwise white, orange-white, cream, pinkish cream, grayish-orange 5B2-3, pale orange white 6A2 developing necropigment near "ochraceous buff" 5A5. Lamellae adnexed to decurrent by a tooth, close to subdistant (L + ll = 35–52; L = 11–16), thickish, with little or no anastomosis but occasionally showing common forking near pileus margin in large basidiomata, becoming crisped in or after drying, seceding and then sometimes appearing pseudocollariate, white to cream white, near "pale olive buff" 3B2, or buff when fresh, developing

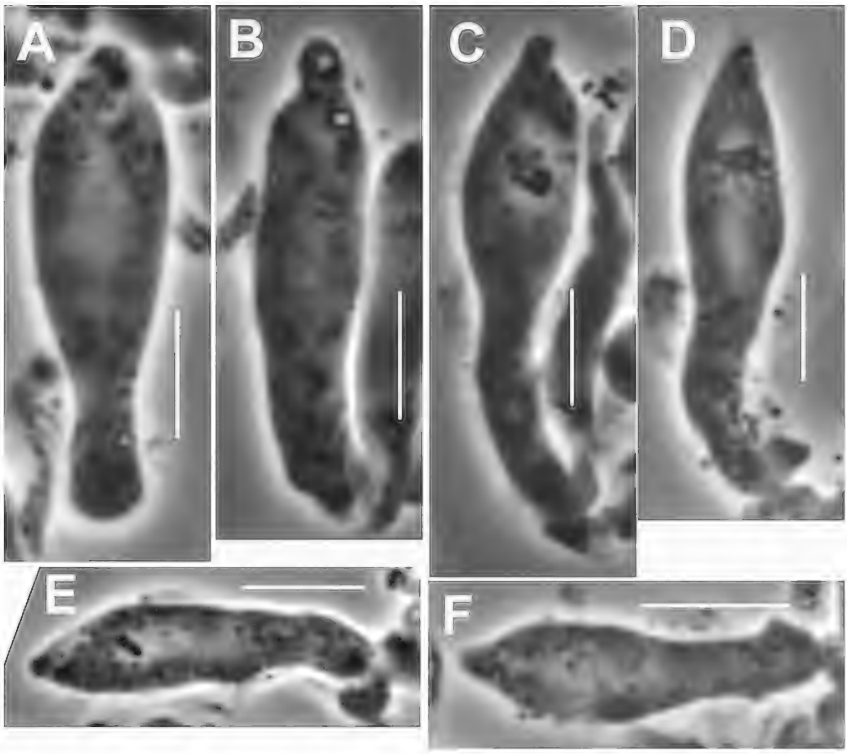


Fig. 25. *Collybiopsis furtiva*. (DED 4410; TENN-F-057309). Pleurocystidia. Note submammillate apices; clamp connection in E. Scale bars = 10 µm.

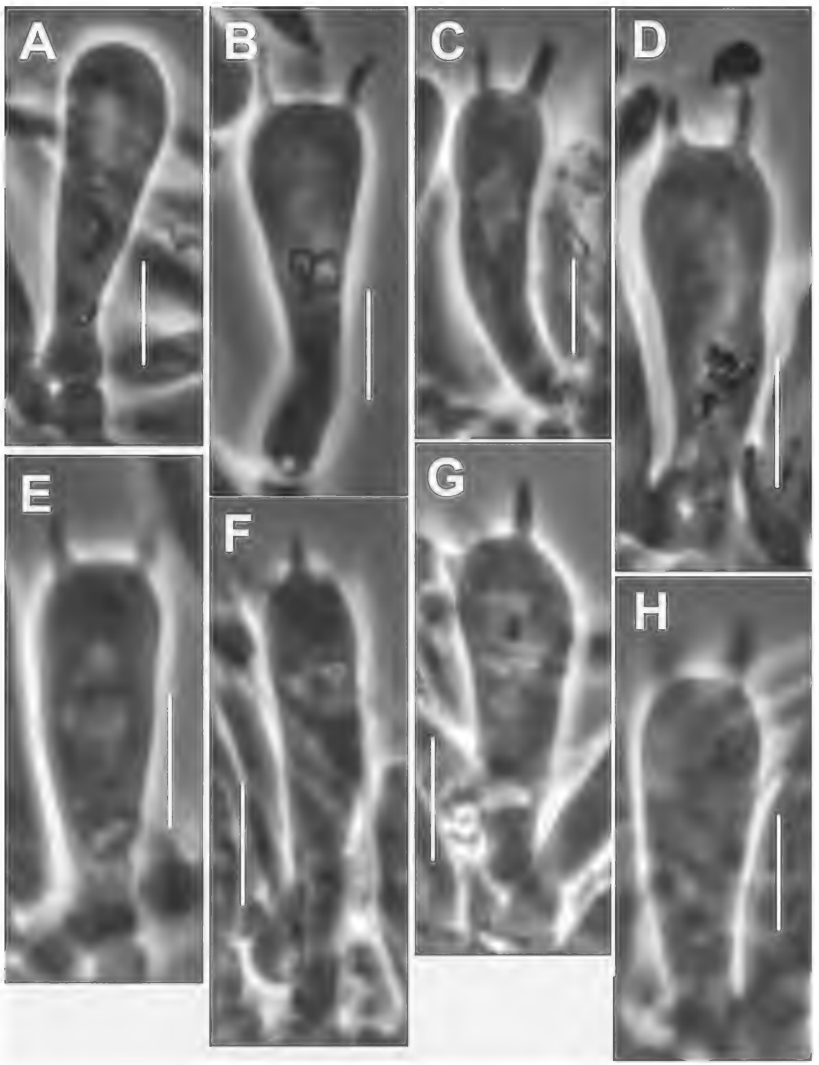


Fig. 26. *Collybiopsis furtiva*. (TFB 11550; TENN-F-059444). Basidioles and basidia. A. Basidiole. B-H. Mature basidia. Note clamp connections in A, D, F. Scale bars = 10 µm.

ruddy necropigment; lamellar edge fimbriate or appearing crystalline, eroded, remaining white to buff or "pale pinkish buff" 6A2, but not marginate when fresh. Stipe 4–11 × 0.3–1.2 mm, terete or somewhat compressed upward,

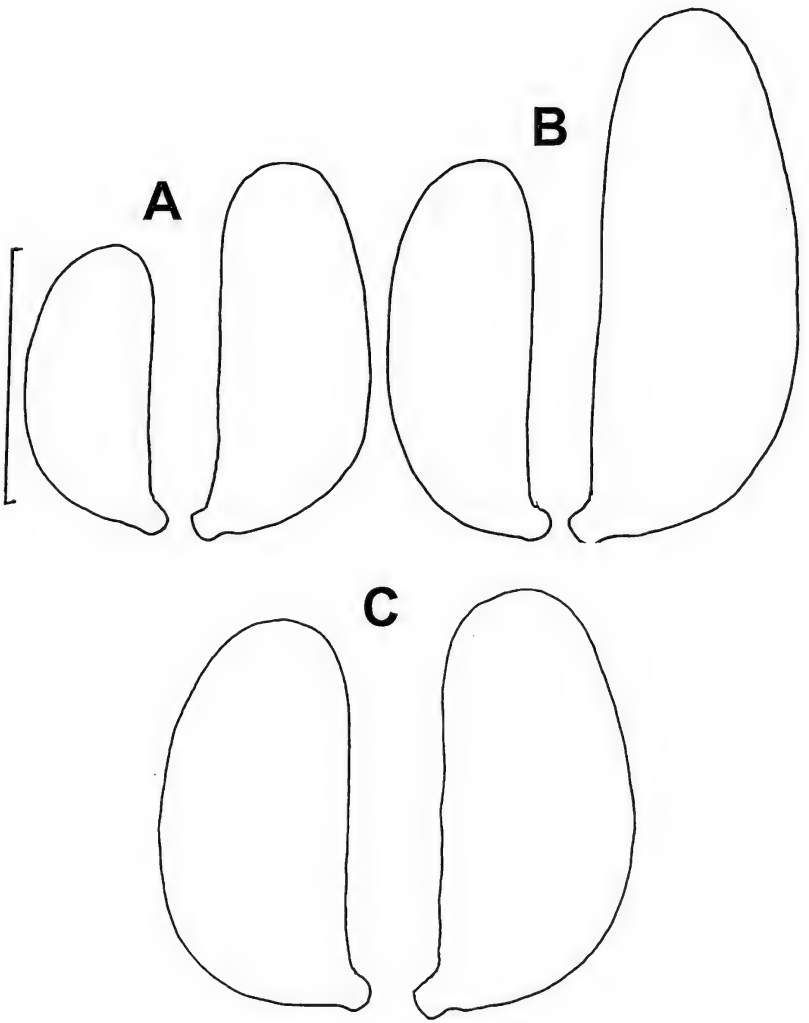


Fig. 27. Basidiospores of *Collybiopsis* taxa.
A. *Collybiopsis furtiva*. (DED 4410; TENN-F-057309).
B. *Collybiopsis furtiva*. (DED 3973; SFSU-F-024523).
C. *Collybiopsis minor*. (TFB 11930; TENN-F-059993).
Scale bars = 10 µm.

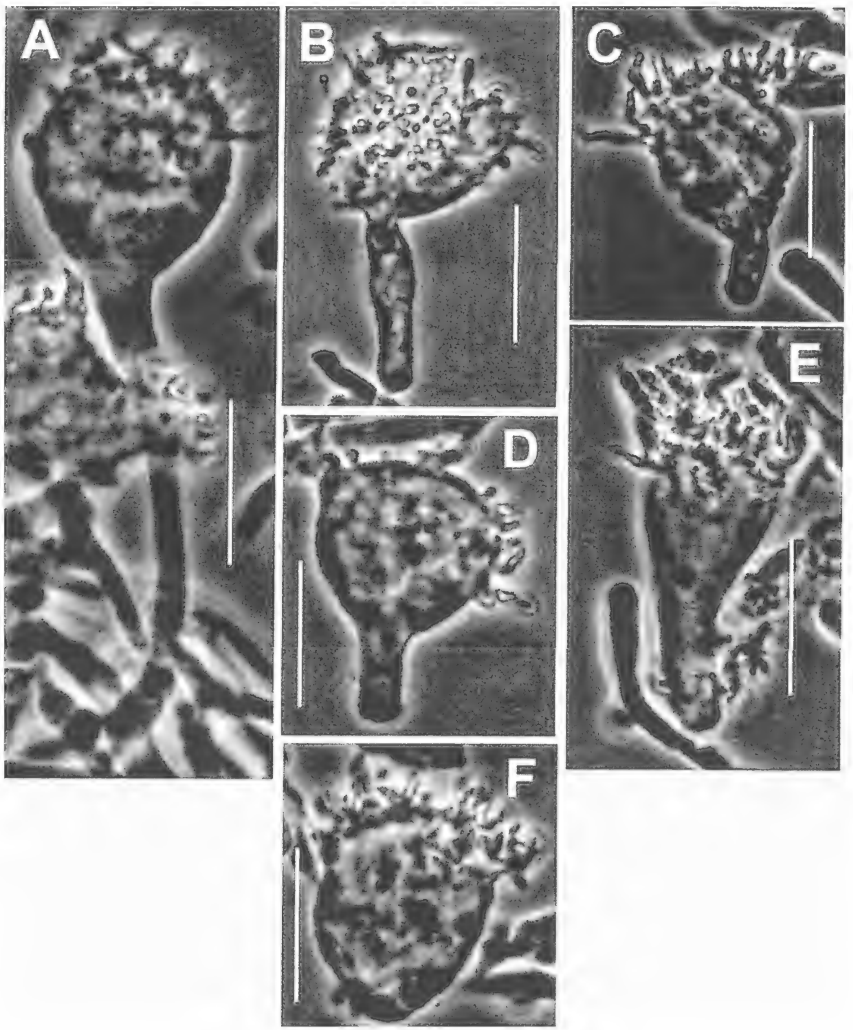


FIG. 28. *Collybiopsis furtiva*. (DED 4425; SFSU-F-024540). Cheilocystidia. Scale bars = 10 µm.

equal or tapered downward and then with minute snow white ring or ruff on stipe base, straight to curved (in drying?), sometimes abruptly pinched at base (similar to adult *Ma. praeacutus*), opaque or (now) appearing subcartilaginous, loosely stuffed to hollow; upper stipe appearing glabrous to minutely flocculose, concolorous with lamellae, not dextrinoid (sallow greenish yellow in IKI + BF);

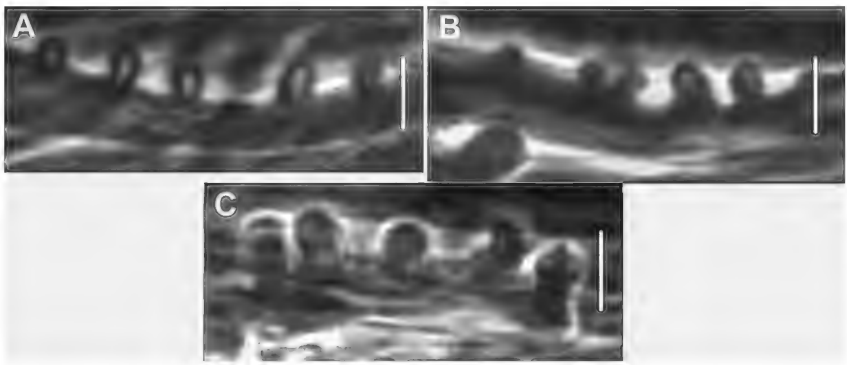


Fig. 29. *Collybiopsis furtiva*. (DED 4410; TENN-F-057309). Upper stipe surface. Note files of simple lobate branches.
Scale bars = 10 µm

lower stipe (basal ~1/5) appearing flocculose to wispy, in age light brown 6D6, "avellaneous" 7B3, reddish brown black to slightly brownish orange 6C5-6when young; insertion appearing insititious. Odor negligible; taste negligible.

Habitat & phenology: Gregarious; fruiting on well-rotted wood and dead twigs of *Rhododendron maximum*, *Tsuga*, various hardwoods, rarely on bark of grape; eastern United States (common in southern Appalachian Mountains); mid-summer.

Pileipellis a well-developed *Rameales*-structure with two types of hyphae: 1) repent hyphae (Fig. 24A, B) 2.5–6.5 µm diam, beset with diverticula; diverticula 1–6.5(–9) × 1–2 µm, appearing stiff, nodulose to strangulate, often dichotomously branched, refringent (PhC); and 2) common hyphal termini (Fig. 24C) otherwise resembling the repent hyphae with similar diverticula. Subpellis including free-form or "antler-shaped" hyphal segments and termini (Fig. 24D-F). Pileus and lamellar tramae loosely interwoven, composed of three hyphal types: 1) hyphae 2.5–6.5(–14) µm diam, firm-walled, conspicuously clamped; 2) basically similar but with long, free-form, hyaline, inflated cells <15 µm diam; and 3) occasional slender hyphae with thickened walls and dense cytoplasm suggestive of gelatinization. Pleurocystidia (Fig. 25) abundant to often scattered, 20–35 × 6–9 µm, hyaline, fusiform, sharply attenuate distally and occasionally submammillate, conspicuously clamped; contents often vaguely partitioned at very apex. Basidioles (Fig. 26A) clavate; basidia (Fig. 26B–H) 20–28 × 6–7 µm, narrowly clavate, not capitulate, 4-sterigmate,

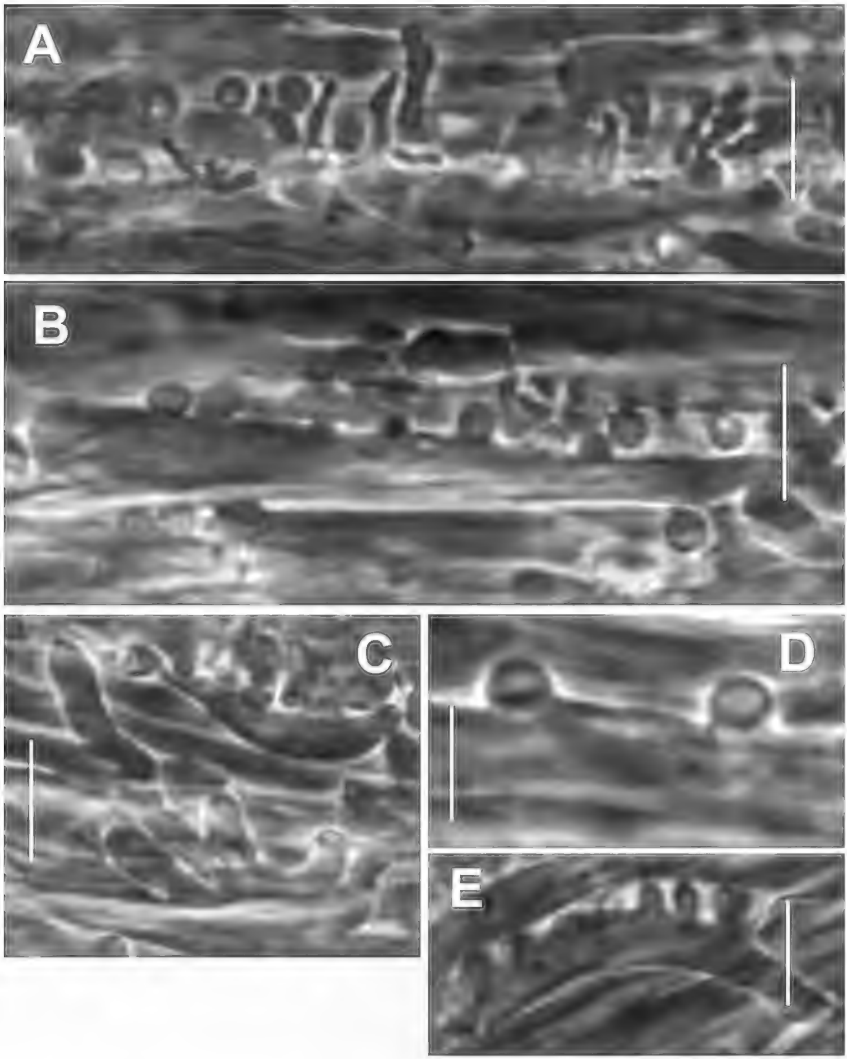


Fig. 30. *Collybiopsis furtiva*. (DED 4410; TENN-F-057309). Lower stipe surface. A, B, E. Files of surface lobate branches. D. Two lobate branches with suggestion of slime matrix. Scale bars = 10 µm.

conspicuously clamped. Basidiospores (Fig. 27A) (6–)6.5–9(–10) × 2.5–3(–3.5) µm (E = 1.86–3.50; E^m = 2.75; L^m = 7.6 µm), elongate-ellipsoid, tapered proximally (marasmioid), thin-walled, hyaline, inamyloid. Cheilocystidia

Fig. 31. *Collybiopsis furtiva.* (DED 3973; SFSU-F-024523). Basidiomata. Scale bar = 10 mm. Photo courtesy of DE Desjardin.

(Fig. 28) hyaline, thin-walled, always obscurely clamped, very variable from clavate (<50 × 10–13 µm) with scattered diverticula over the apical 15–20 µm, shorter (base not seen), branched (branches 6-8 µm broad, variably diverticulate) to ventricose-rostrate, stalked (<50 µm long) with apical inflation <20 µm broad, smooth or beset with diverticula varying from papillate (*rotalis*-like) to tentacular (<10 × 1–1.5 µm). Upper stipe medulla consistent with medulla of lower stipe (see below); upper stipe cortical hyphae also similar, but surface lobate branches (Fig. 29) seem consistently simple, knobby, not vermiform, perhaps thick-walled, subrefringent. Lower stipe medulla in minimal slime matrix. Hyphae of two types: 1) broad, 4–7.5 µm diam., hyaline, thick-walled (wall <2.5 µm thick with evidence of individual gelatinization), obscurely clamped; and 2) slender, 1.5–3 µm diam., firm- to thick-walled, conspicuously clamped, occasionally with incomplete clamps (i.e., small, curved, hook-like branches). No tissue dextrinoid. Lower stipe cortical hyphae (Fig. 20) 3.5–7.5 µm diam, thick-walled, pigmented (ochraceous brown), producing small, thickly scattered, hyaline, thin-walled, nodulose to vermiform branches (caulocystidia; Fig. 29) 3.5–6.5 µm broad. Caulocystidia of two types: 1) digitate or peg-like individuals (Fig. 30A, B, E) arising from cortical hyphae as side branches, 4–13 × 2.5–4 µm; and 2) cheilocystidia-like (Fig. 30D), with inflated portions surmounted by numerous lobe-like diverticula.

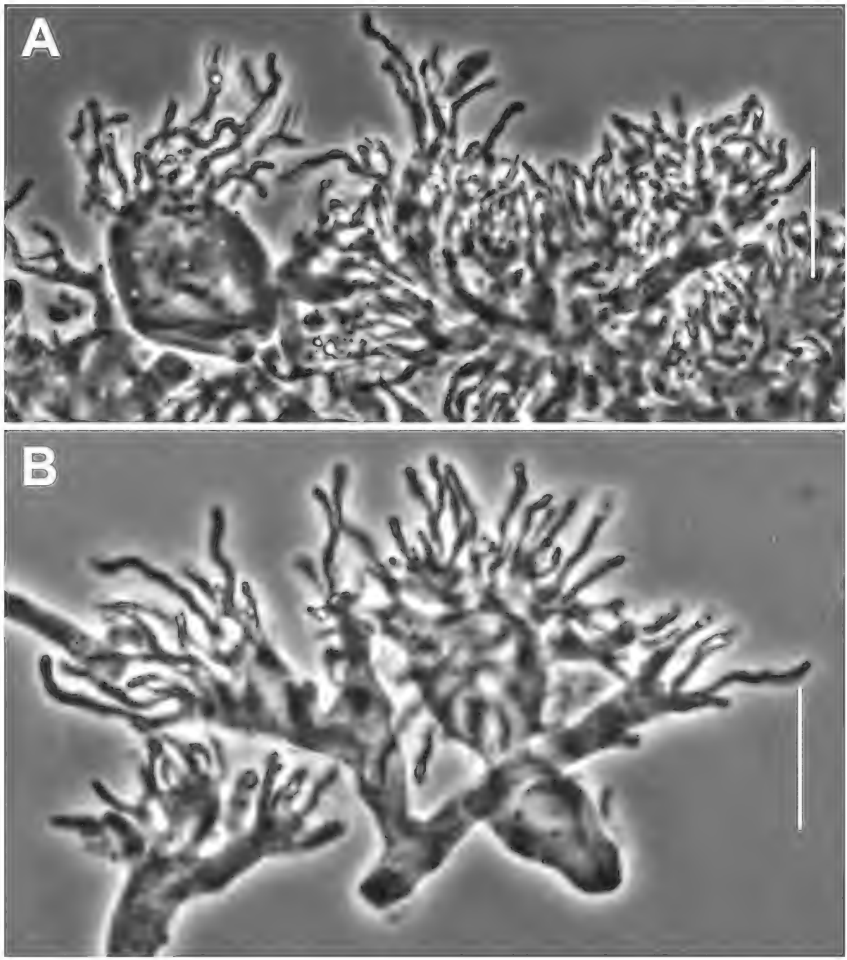


Fig. 32. *Collybiopsis furtiva*. (DED 3973; SFSU-F-024523). Cheilocystidia. A. Cluster of cheilocystidia. B. Clavate individual plus divaricately branched individual. Scale bars = 10 µm.

Commentary: Most synonyms listed under *Agaricus ramealis* in Index Fungorum are homotypic (i.e., based on Bulliard's basionym). The European neotype designated by Antonín & Noordeloos (1993; France, Calais, Boulogne, Noordeloos 7310, L) serves to establish the taxonomic basis of these homotypic synonyms. Although numerous subspecies and varieties have been proposed, none have been explicitly based on North American material.

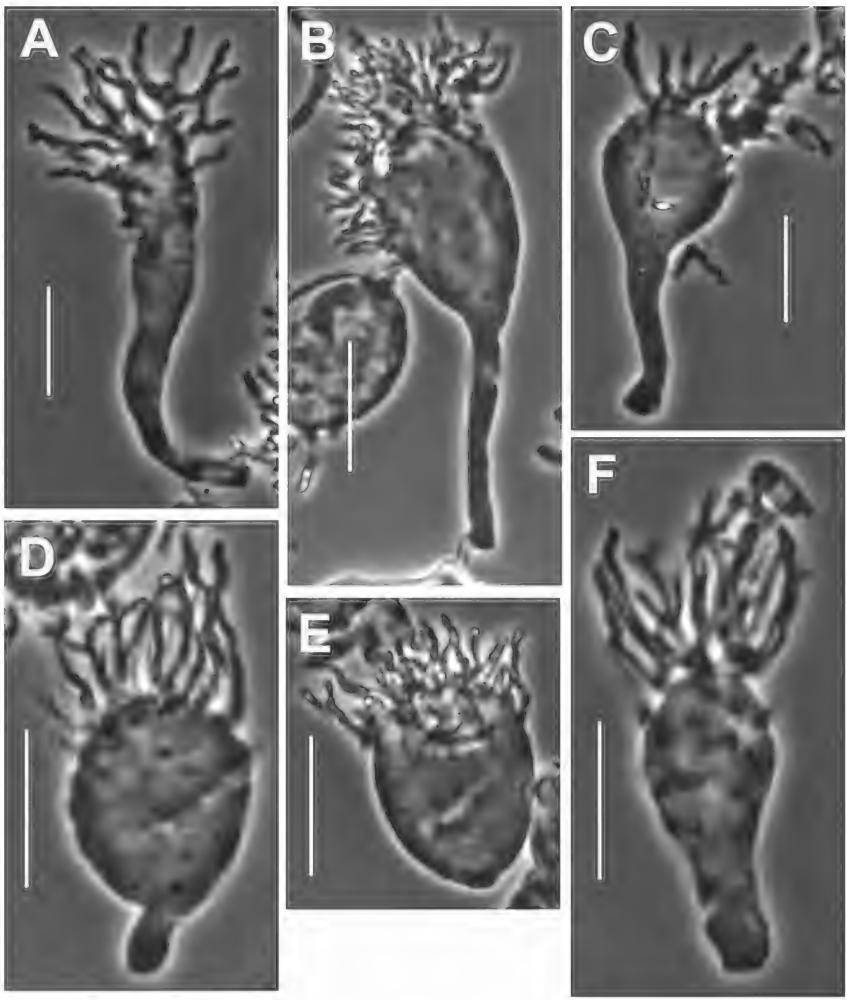


Fig. 33. *Collybiopsis furtiva*. (DED 3972; SFSU-F-024523). Ventricose-rostrate cheilocystidia. Note prominent diverticula. Scale bars = 10 µm.

In order to reach *Marasmiellus ramealis* in Desjardin's (1997) key to the genus in the southern Appalachian Mountains, the following characters are required (some a poor match to the description above): 1) basidiospores <10.5 µm long; 2) stipe central, habit marasmioid, collybioid or mycenoid, basidiomata NOT pleurotoid, not on monocots; 3) stipe base NOT attenuated to a narrow point, odor not alliaceous nor fetid; 4) pileipellis a

well-developed *Rameales*-structure; 5) pileus pigmented overall (including pinkish brown); 6) rhizomorphs absent; 7) pileipellis lacking inflated terminal cells; 8) pileus yellowish brown vs dark brown to brown (separating from *Ma. nodosus*); 9) context <1 mm thick (vs. context 2–4 mm thick); 10) stipe 0.2–1 mm diam. (vs. stipe 2–3(–11) mm diam.; 11) basidiospores 2.5–4.5 µm broad (vs 4.5–7 µm broad); 12) cheilocystidia broadly clavate with numerous fine diverticula (vs cheilocystidia irregular in outline, often contorted, and with nodulose outgrowths); and 13) basidiomata formed on epigeous branches and stems of deciduous trees, shrubs or herbaceous dicots (vs basidiomata formed on hypogeous sticks or roots). According to Desjardin (1997), southeastern North America *M. ramealis* is most commonly confused with *Marasmius* (now *Mycetinis*) *opacus* with larger basidiomata and plentiful white rhizomorphs and rather different pileipellis (see Petersen & Hughes 2017b). Our observations indicate also a resemblance to *Ma. praeacutus*, distinguished in the field by its pinched stipe and common, persistent basidiomatal primordia.

Stipe surface ornamentation, especially upper stipe, comprises scattered lobes or nodes, more complex on lower stipe. When simple, such nodules are subrefringent, identical with diverticula of cheilocystidia and especially pileipellis *Rameales*-structure.

Parenthetically, it is interesting to know Earle's taxonomic concept of *Marasmius ramealis*. Specimen Earle 767 (collected on N.Y. Botanical Garden grounds and identified by Earle; NY) may be representative. Although microscopic structures are collapsed, diagnostic characters do not totally agree with those of eastern North American *Co. "ramealis"* (see above). No attempt has been made to extract DNA.

We need to note here an abnormal collection of *Co. furtiva* (DED 3973, SFSU-F-024523 as *Ma. ramealis*), collected in the same general area as several other species. Significantly, its nrITS sequence does not differ from those of several other *Co. furtiva* collections, yet the basidiomata (Fig. 31) are anatomically distinct, particularly the cheilocystidia and stipe ornamentation. In DED 3973 cheilocystidia (Figs. 32, 33) 45–60 × 9–19 µm (at widest point), appear to arise deep in the hymenophoral trama (surely longer than basidia or pleurocystidia); are ventricose-rostrate, stalked with an inflated terminus, and rarely branched; and include scattered small, broadly clavate individuals; the stalks (25–40 × 3–5.5 µm) are conspicuously clamped, thin-walled, easily distorted or disarticulated with termini that are inflated, thin-walled, unpigmented, and beset with

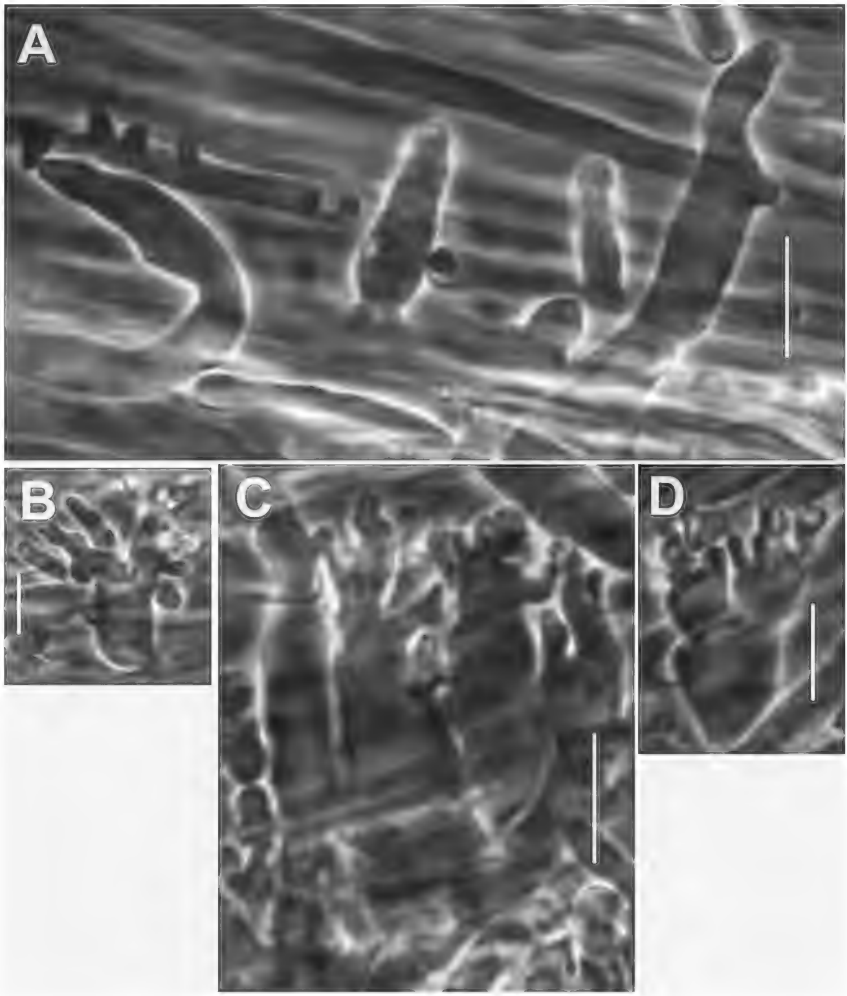


Fig. 34. *Collybiopsis furtiva*. (DED 3973; SFSU-F-024523). Caulocystidial structures. A. Individual caulocystidia. B-D. Coralloid, cheilocystidial structures. Scale bars = 10 µm.

numerous (<70) medusoid diverticula; the slender long diverticula (<25 × 1–1.5 µm) are usually elongate-digitate but occasionally dichotomously branched, gnarled, subnodulose, and often apically refringent (PhC). Basidiospores (Fig. 27) are significantly larger than those of *Co. furtiva*. The stipe ornamentation consists of both individual hyphal caulocystidia and coralloid cheilocystidial structures; individual hyphal caulocystidia

(Fig. 34A) 6–75 × 5–9 µm, thick-walled (wall <2 µm thick, pallid greenish ochraceous PhC), sometimes appearing in "picket fence" files, broadly rounded to setoid with sharply acute apex; caulocystidia resembling cheilocystidia (Fig. 34B-D) 15–45 × 9–15 µm, coralloid with peg-like or capitulate diverticula, thick-walled (wall <1 µm, hyaline). Lower stipe ornamented with accumulated heaps of mixed caulocystidial structures.

Probably coincidentally, the submammillate pleurocystidial apices of *Co. furtiva* resemble those of an unidentified *Collybiopsis* (TFB 23217; TENN-F-023217) close to *Gymnopus subnudus* in *G.* sect. *Vestipedes* (Fig. 1).

Cheilocystidia of DED 3973 resemble those of *Co. californica* (q.v.) but our molecular nrITS phylogeny (Fig. 2) places its sequence with other southeastern collections typical of *Co. furtiva*. Coralloid cheilocystidial stipe vesture elements seem unique.

Additional specimens examined: **USA, Georgia, Rabun Co.**, vic. Clayton, Warwoman Dell Picnic Area, 34°52′58″N 83°20′58″W, 6/15/1992, coll. SA Gordon, TFB 4796 (TENN-F-051097). **New York, Bronx Co.**, "Bronx Woods," det. WA Murrill, VIII.1911 (02755903 NY). **North Carolina, Macon Co.**, vic. Highlands, Bull Pen Rd., 28.VII.1987. coll. TJ Baroni, det. DE Desjardin, DED 4410 (TENN-F-057309); vic. Highlands, Horse Cove, Rustic Falls area, 12.VII.1984, coll. & det. DE Desjardin, DED 4584 (SFSU-F-024508); vic. Highlands, Cliffside Lake Campground, 29.VII.1986, coll. & det. DE Desjardin, DED 3973 (SFSU-F-024523); 35°02′24″N 83°27′12″W, 30.VI.2002, coll. RHP, TFB 11558 (TENN-F-059444); vic. Otto, Coweeta Hydrologic Laboratory, Ball Creek Rd., 26.VI.1993, coll. & det. DE Desjardin, DED 5796 (SFSU-F-024524). **Tennessee, Blount Co.**, GSMNP, Cades Cove, 35°35′39″N 83°50′31″W, 15.VI.1957, coll LR Hesler, TFB 7867 (TENN-F-007867).

Collybiopsis hasanskyensis R.H. Petersen, **sp. nov.** Figs. 35-41

IF 557072

Differs from other *Collybiopsis* taxa by its diminutive basidiomata that fruit on *Alnus* twigs and strobili; its unique ITS sequence; its gymnopoid pileipellis lacking a *Rameales*-structure; its stalked-clavate, smooth to lobate to diverticulate cheilocystidia that are larger than basidia and pleurocystidia, and its pale buff necropigment.

Type: Russia, Primorsky krai, Hasansky Dist., vic. Primorsky, Kedrovaya Reserve, 43°05.87′N 131°33.57′E, 18.VIII.2005, coll RHP, A. Kovalenko, TFB 11846 (Holotype, TENN-F-060730).

Etymology: Hasansky; district in Primorsky Region of Russia, where the holotype was collected.

Basidiomata (Fig. 31A) diminutive. Pileus 4–8 mm broad, plane to somewhat depressed with involute margin, matt, delicately radially wrinkled, inward "pinkish buff" 6A3, outward "pale cinnamon pink" 5A2, becoming

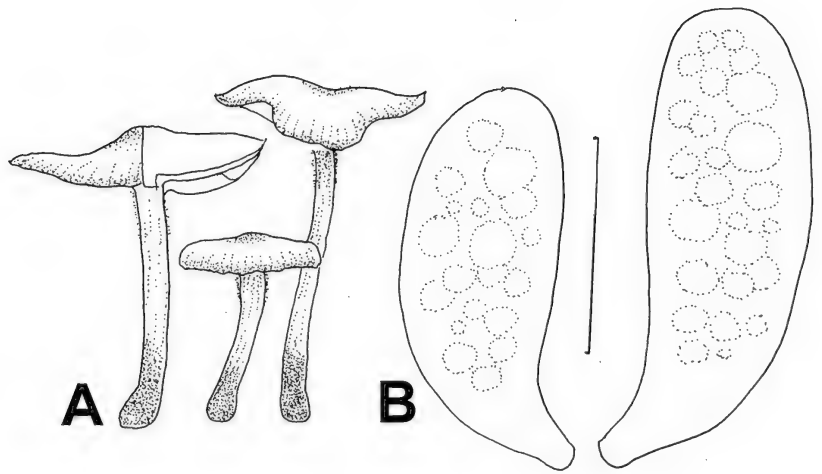


Fig. 35. *Collybiopsis hasanskyensis*. (TFB 11846; TENN-F-060730).
A. Basidiomata B. Basidiospores Scale bar: A = 5 mm; B = 5 µm.

off-white with pale cantaloupe-colored necropigment; pileus context thin, brittle when dried, white. Hymenophore developing a pallid cantaloupe necropigment. Lamellae adnate to shallowly decurrent, subdistant to distant, varying from knife-like and then occasionally ventricose (<0.5 mm broad), to reduced to thin pleats, rarely with dichotomy but often buttressed or cross-veined, color unchanged from fresh (off-white with pinkish tint), L + ll = (22–)36–40, L = (9–)12–16, off-white with pinkish tint. Stipe 6–9 × 0.6–0.8 mm, equal to tapering somewhat upward, sometimes with base slightly enlarged to club-shaped, inserted only at base of club, apically minutely roughened (60×), soon appearing glabrous, now cartilaginous (glabrous-shining), pale apically, "sayal brown" 6C5 to dirty grayish brown downward, developing rich cantaloupe necropigment uniformly, consistently with small, off-white, circular, appressed basal pad. Odor and taste negligible. Rhizomorphs not observed.

Habitat & distribution: Fruiting on dead *Alnus* twigs and strobili; late summer and early autumn; presently known only from Hasansky District of far-eastern Russia near North Korea.

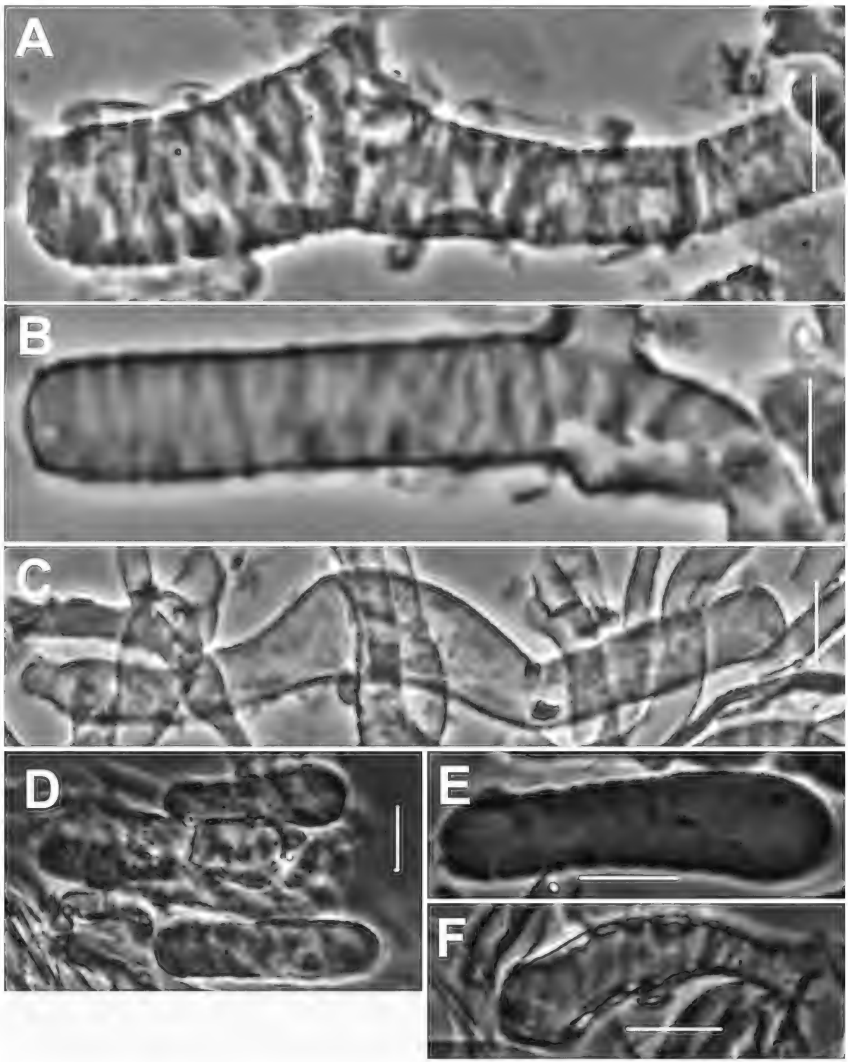


FIG. 36. *Collybiopsis hasanskyensis*. (TFB 11846; TENN-F-060730). Pileipellis hyphae. A. Heavy annular ornamentation. B. Weak annular ornamentation. C. Hypha with dense contents. D, E. Roughened, "cigar-shaped" hyphal segments. F. Thick-walled hypha with substantial profile calluses. Scale bar 10 μm.

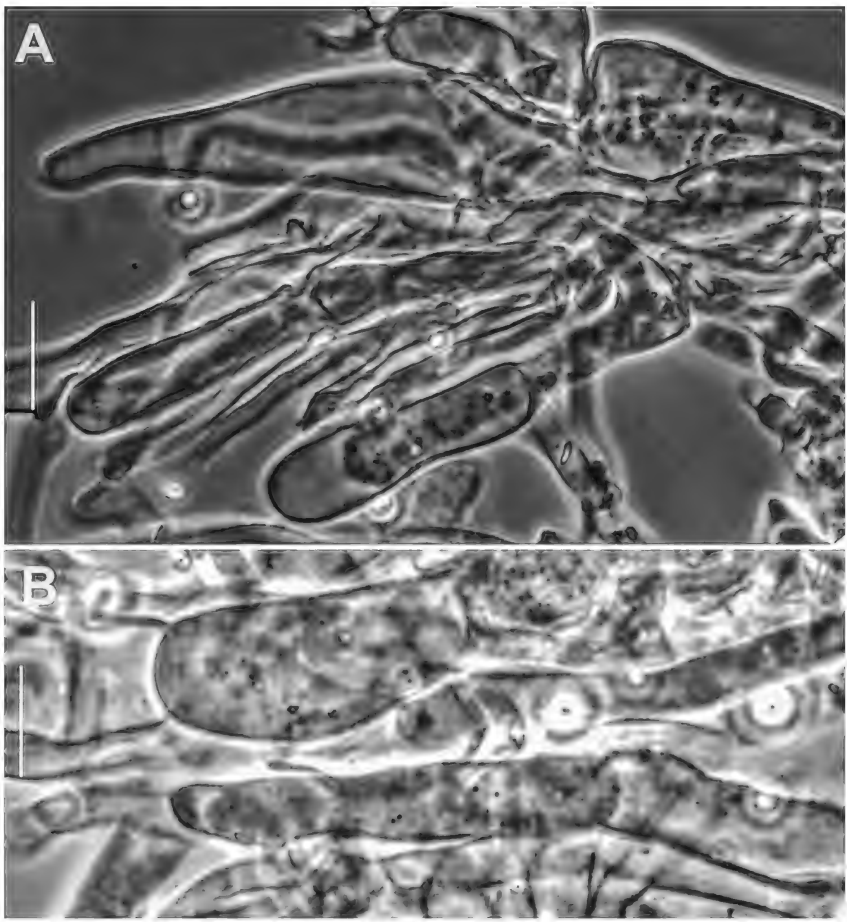


Fig. 37. *Collybiopsis hasanskyensis*. (TFB 11846; TENN-F-060730). Lamellar trama. A. Trama, showing inflated hyphae. B. Hyphal fragments with dense contents. Scale bar = 10 µm.

Pileipellis a repent layer of hyphae 4.5–13 µm diam, of several types: 1) thin-walled, without ornamentation, conspicuously clamped; 2) firm- to thick-walled (wall <1 µm thick, hyaline), ornamented (Fig. 36C) with two types of thickening; a) hardly visible in profile but vaguely annular in face view (Fig. 36B); b) prominent in profile view with conspicuous profile calluses (Fig. 36F); profile calluses <1.5 µm thick, lens-shaped, hyaline, refringent, conspicuously clamped; 3) disarticulated, somewhat inflated cells, cylindrical or cigar-shaped, thick-walled (wall <1 µm thick),

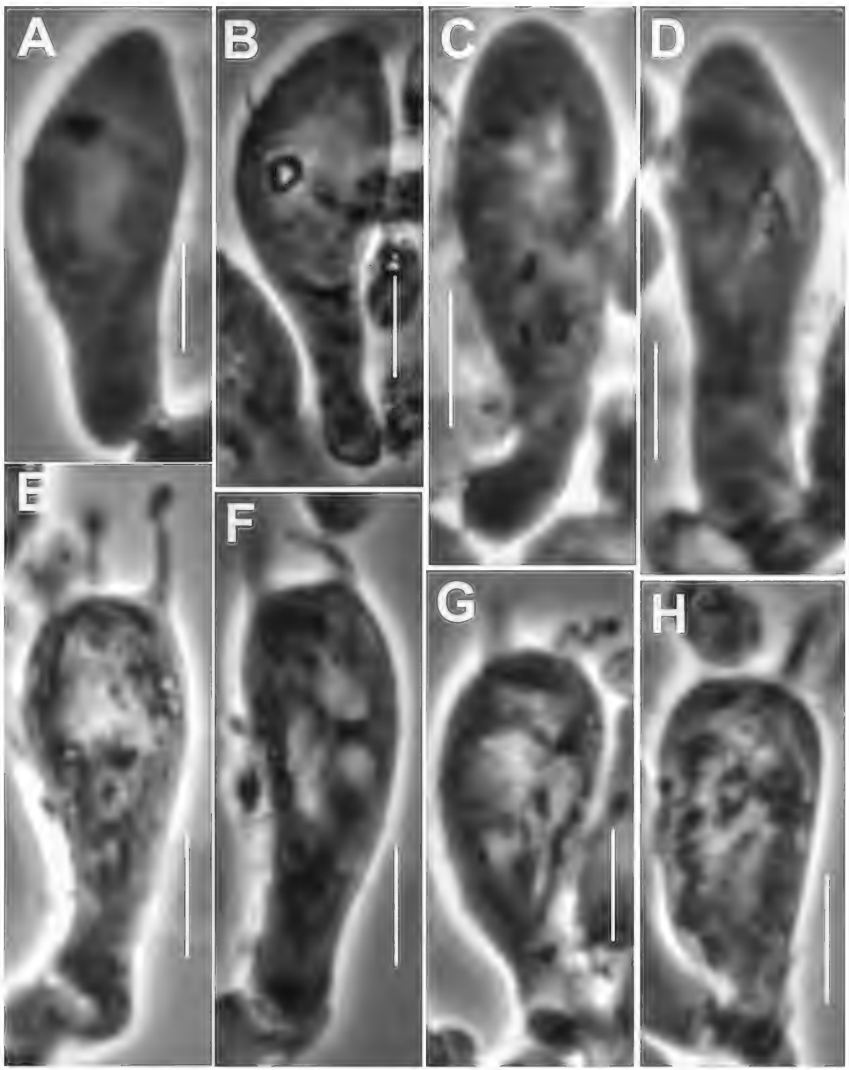


Fig. 38. *Collybiopsis hasanskyensis*. (TFB 11846; TENN-F-060730). Hymenial structures. A-D. Pleurocystidia. E-H. Basidia. Note clamp connection in E. Scale bar = 10 µm.

delicately ornamented in gregarious plaques (Fig. 36D, E); and 4) repent, thin-walled hyphae 4–8 µm diam, heavily ornamented with pigmented plaques, perhaps crystalline, protruding from the hyphal wall angularly <4 µm high (Fig. 36A). Note: no evidence of *Rameales*-structure. Pileus and

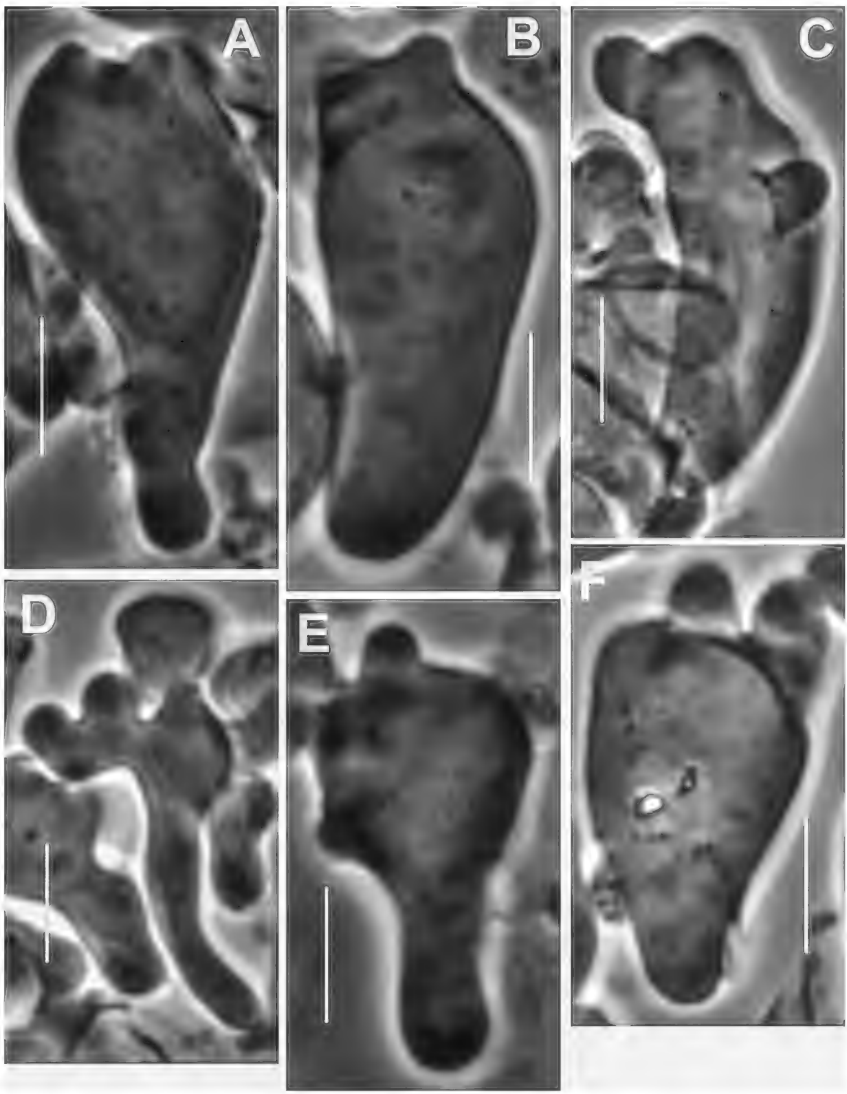


Fig. 39. *Collybiopsis hasanskyensis.* (TFB 11846; TENN-F-060730). Typical cheilocystidia. Scale bars = 10 µm.

lamellar trama interwoven (Fig. 37), more tightly so under hymenophore; hyphae 3–6.5(–14) µm diam, firm-walled, hyaline, without slime sheath or matrix, conspicuously clamped. Subhymenial hyphae seem to disintegrate

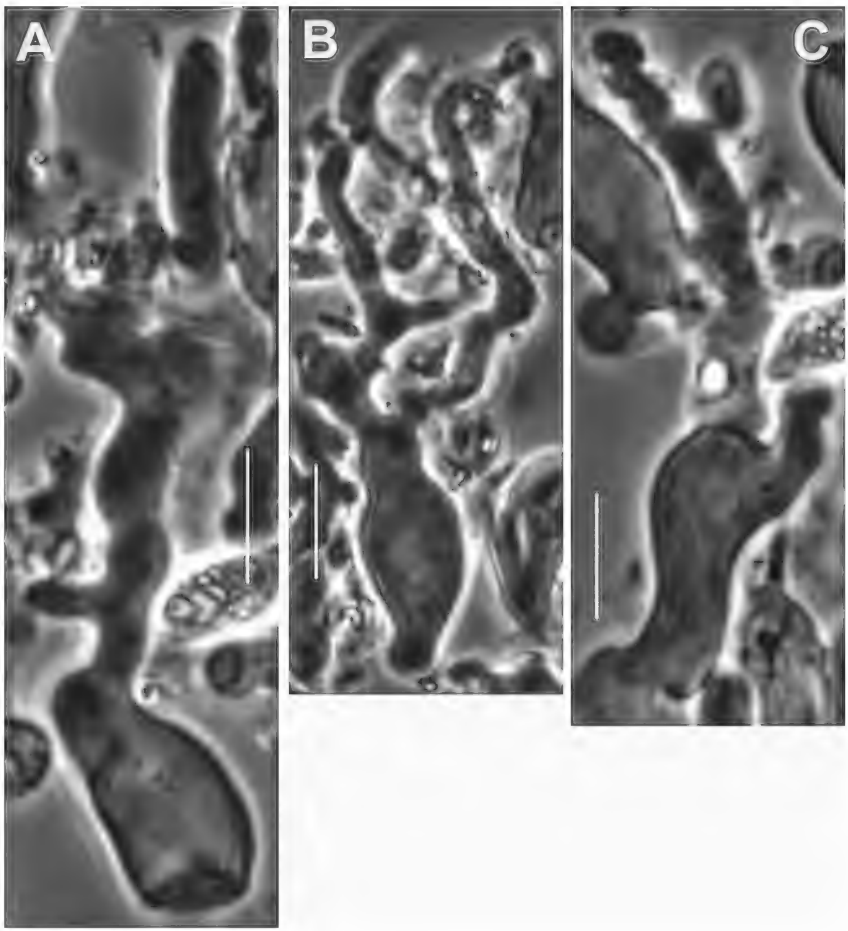


Fig. 40. *Collybiopsis hasanskyensis.* (TFB 11846; TENN-F-060730). Diverticulate cheilocystidia. Scale bars = 10 μm.

into debris, persistent after hymenial discharge making observation of basal clamps in the hymenium difficult. Evidence of gelatinization absent. Pleurocystidia (Fig. 38A–D) common, not abundant, stalked-fusiform, 19–22 × 9–11 μm at widest point, inconspicuously clamped; contents more or less homogeneous, not partitioned. Basidia (Fig. 38-H) digitate to clavate but not subcapitulate, 18–23 × 9–11 μm, occasionally suburniform, 2–4-sterigmate, inconspicuously clamped; sterigmata slender, lyre-shaped;

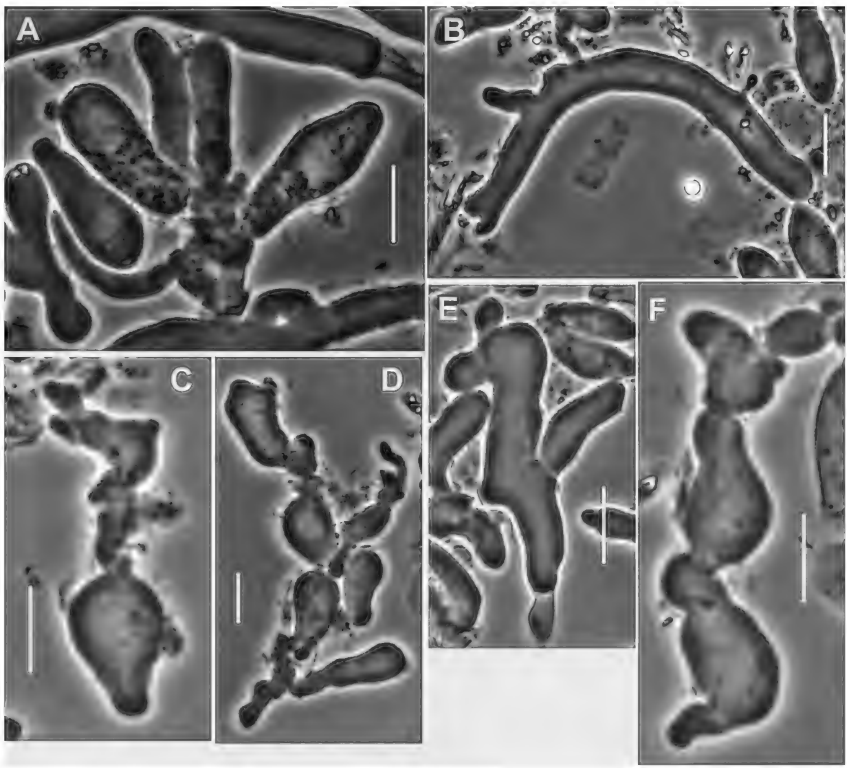


Fig. 41. *Collybiopsis hasanskyensis*. (TFB 11846; TENN-F-060730). Caulocystidia. Scale bars = 10 μm.

contents heterogeneous, multi-granular with amorphous inclusions. Basidiospores (Fig. 35B) 7–11 × 3.5–4.5(–5.5) μm (E = 1.82–2.75; E^m = 2.29; L^m = 8.8 μm), elongate-ellipsoid, widely rounded distally, tapered proximally (marasmioid), thin-walled, hyaline, inamyloid; contents heterogeneous, foamy (i.e. multiguttulate). Cheilocystidia (Fig. 39) abundant at lamellar edge, apparently easily disarticulated from basal septum (i.e., appearing without parent hyphae and with no evidence of clamp connection), firm- to thick-walled (wall <1 μm thick, hyaline, usually on emergent portion, not portions juxtaposed to other hymenial elements), very variable in shape from subglobose and without lobes, broadly clavate with expanded distal portion with one or few lobes, to columnar, to stalked with distal portion moderately expanded by with almost equal lobes, to occasionally grown out

distally to form stout diverticula (Fig. 40); diverticula ≤40 × 3–5 µm, often lobed and occasionally branched; measurements really only approximate because forms are so variable, 30–42(–60) × 7–11 µm (at widest point), hyaline, often appearing empty (see photos). Stipe anatomy: no apparent differentiation of medullary versus cortical hyphae, all 4–6 µm diam, firm-walled (not thick-walled), obscurely clamped, apparently uniformly dextrinoid (cut ends of medullary hyphae just as dextrinoid as corticals); clamp connections, if present, inconspicuous. Stipe surface possibly with very thin slime matrix. Stipe apex with covering of inflated, free-form caulocystidia similar to inflated and distorted pleurocystidia (normal pleurocystidia and cheilocystidia common in this caulocystidial covering, some with tentacular apical outgrowths). Caulocystidia (Fig. 41) (15–)20–40(–55) × (3-tentacular outgrowth) 8–14 µm, simple inflated utriform structures with almost invisible pedicel to repeatedly constricted "chains," occasionally a combination of tentacular and constricted structures. Lower stipe glabrous.

Commentary: Although *Collybiopsis ramealis* exhibits a typical *Rameales*-structure pileipellis (as the archetype of the structure), this construction is not universal even in the *Co. ramealis* complex. Singer (1973) included nearly 20 Latin American taxa in *M.* subsect. *Ramealini*, but several did not exhibit the characteristic setulose repent hyphae and broom cell-like hyphal termini, and some were described as having a trichodermium of "thorny" or setulose hyphae. [*Marasmiellus foliiphilus* Dutta & al. (2015) was described and illustrated with such a trichodermium.] Likewise, *Co. hasanskyensis* lacks *Rameales*-structure in the pileipellis, instead showing typical gymnopoid repent hyphae, often with annular ornamentation.

Fig. 1 (ITS + LSU-based phylogeny) places *Co. hasanskyensis* sister to *Co. vaillantii* in the larger clade including *Co. eneficola* and *Co. biformis*.

Additional specimen examined: **RUSSIA, Primorski krai, Hasansky Dist.**, vic. Primorsky, Kedrovaya Reserve, 43°05.87′N 131°33.57′E, 18.VIII.2005, coll. RHP, TFB 11847 (TENN-F-60731).

Collybiopsis minor R.H. Petersen, **sp. nov.** Figs. 42-49

IF 556206

Differs from other *Collybiopsis* taxa by its habit on dead *Tsuga* twigs; its unique ITS rDNA molecular sequences; its pileipellis a repent layer of interwoven, non-diverticulate hyphae, often encrusted with annular deposit; its complete absence of gelatinized tissue; its pallid vestured stipe; and its conspicuously clamped hyphae (including hymenophore elements).

Fig. 42. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Dried basidiomata on *Tsuga* twigs. Scale bar = 10 mm.

Type: USA, Tennessee, Blount Co., GSMNP, Turkey Pen Ridge trailhead, 35°36′47″N 83°43′37″W 18.VI. 2004, coll. RHP, TFB 11930 (**Holotype**, TENN-F-059993).

Etymology: *Minor* = small, referring to the size of basidiomata.

Basidiomata (Fig. 41) diminutive. Pileus 4-9 mm broad, applanate, usually with down-curved margin, occasionally with shallow umbo, matt; disc and inner limb "army brown" 8D5 to "wood brown" 7C4; outer limb and margin "vinaceous buff" 9B2 to "tilleul buff" 7B2 (in drying remaining not far from "avellaneous" 7B3), not at all sulcate-striate; margin irregular as though eroded. Lamellae close (L + ll = 60-68; L = 20-24), adnexed (but without pseudocollarium), thin, subventricose (<1 mm broad), off-white when fresh, drying pallid yellowish with no necropigment; edges entire, somewhat paler than face; lamellulae in 2–3 ranks, plentiful at pileus margin. Stipe 8–15 × 1–1.5 mm, concolorous with pileus (more or less "avellaneous" 7B3) to somewhat more pallid or off-white where vestured, terete, equal or slightly tapering upward (base thicker than apex), lightly stuffed, vestured throughout; stipe base with conspicuous white ruff <0.5 mm high; insertion

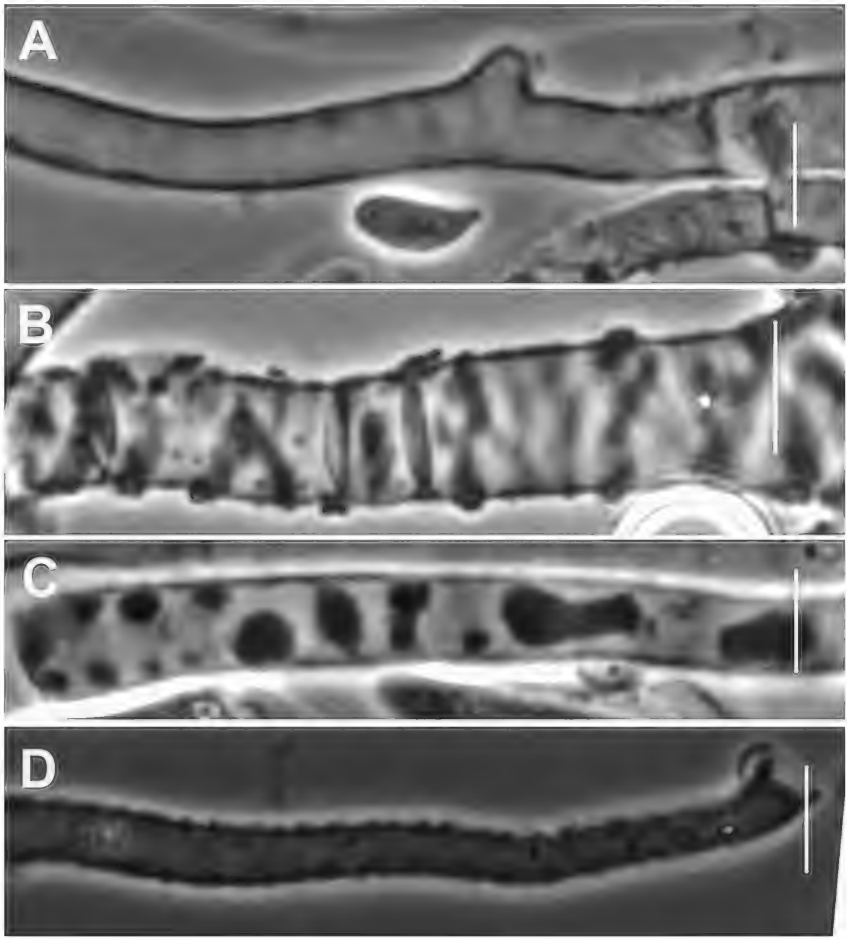


Fig. 43. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Pileipellis elements. A. Smooth, repent hyphae (note basidiospore); B. Hyphae with annular ornamentation; C. Hypha with contents appearing oily; D. Slender hyphae with minute roughening; note clamp connection at right. Scale bars = 10 μm.

not insititious. Rhizomorphs sporadic, white, ropy (not well-defined), associated with resupinate white pad. Taste and odor negligible.

Habitat & phenology: Four collections known, all fruiting on very slender dead twigs of *Tsuga* in southern Appalachian Mountains (Tennessee, South Carolina); June-July.

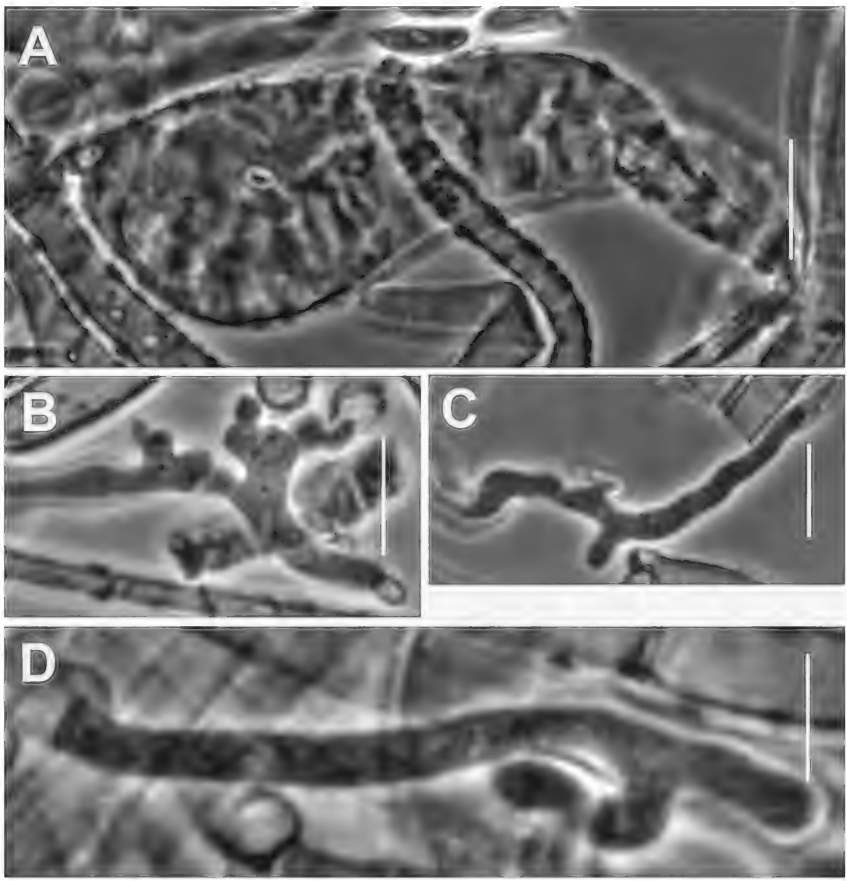


Fig. 44. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Pileipellis and subpellis hyphae. A. Inflated, ornamented hyphal segment of pileipellis; B-D. Slender, meandering hyphae of subpellis, with occasional lobate side branches. Scale bars = 10 µm.

Pileipellis an interwoven repent layer with no evidence of slime deposition, constructed of the following: 1) repent, unoriented hyphae 3–8.5 µm diam, firm-walled, conspicuously clamped, ranging from smooth (Fig. 43A) to ornamented; ornamentation ranging from a) scattered spiculate "crystals," unoriented; b) annular or striped ornamentation (Fig. 43B) of varying density and width (profile calluses <1 µm thick); contents hyaline, speckled (Fig. 43C) as though oily, to dense and then hypha usually slender (Fig. 43D); 2) inflated hyphal segments (Fig. 44A) <16 µm diam,

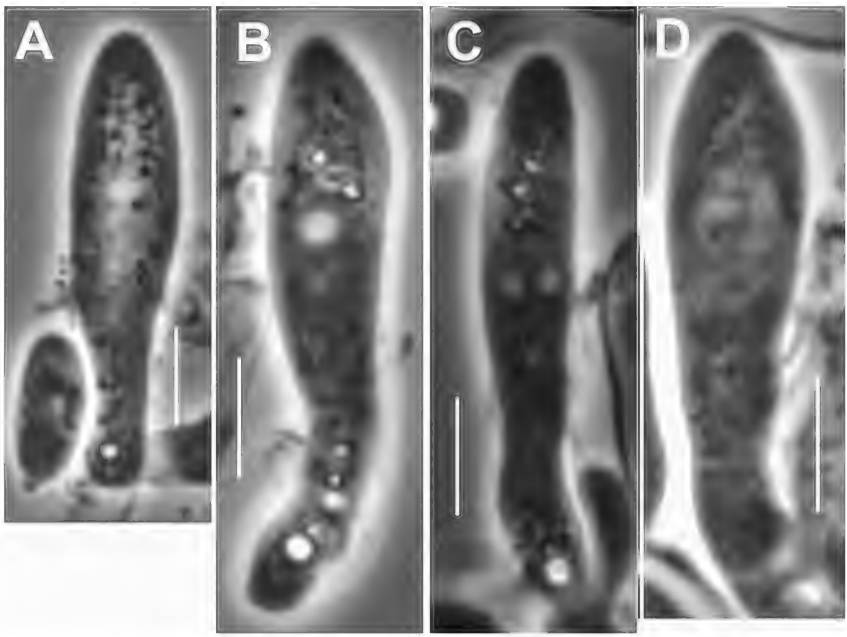


Fig. 45. *Collybiopsis minor*. (TFB 11930; TENN-F-059993).
Pleurocystidia (note basidiospore in A). Scale bars = 10 μm.

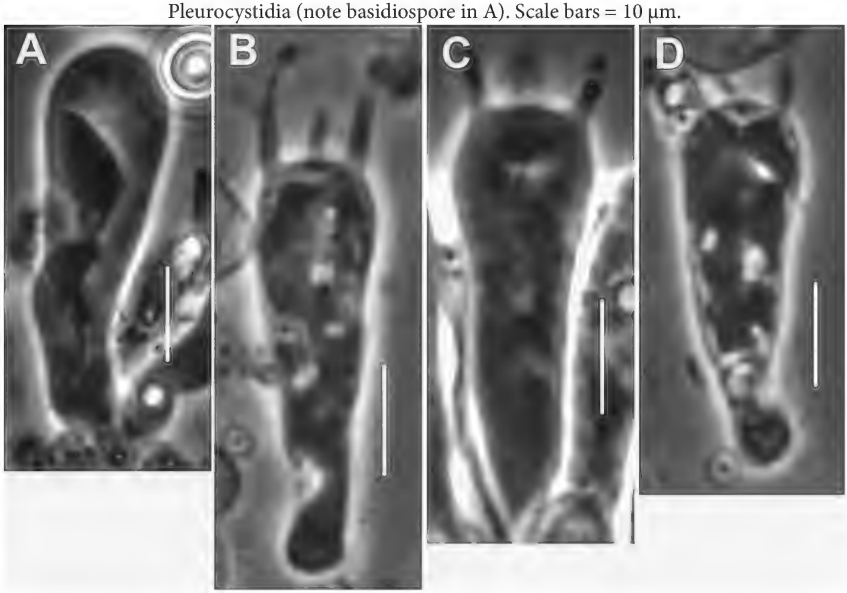


Fig. 46. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). A. Basidiole. B-D. Mature basidia.
Note non-refringent, heterogeneous contents. Scale bars = 10 μm.

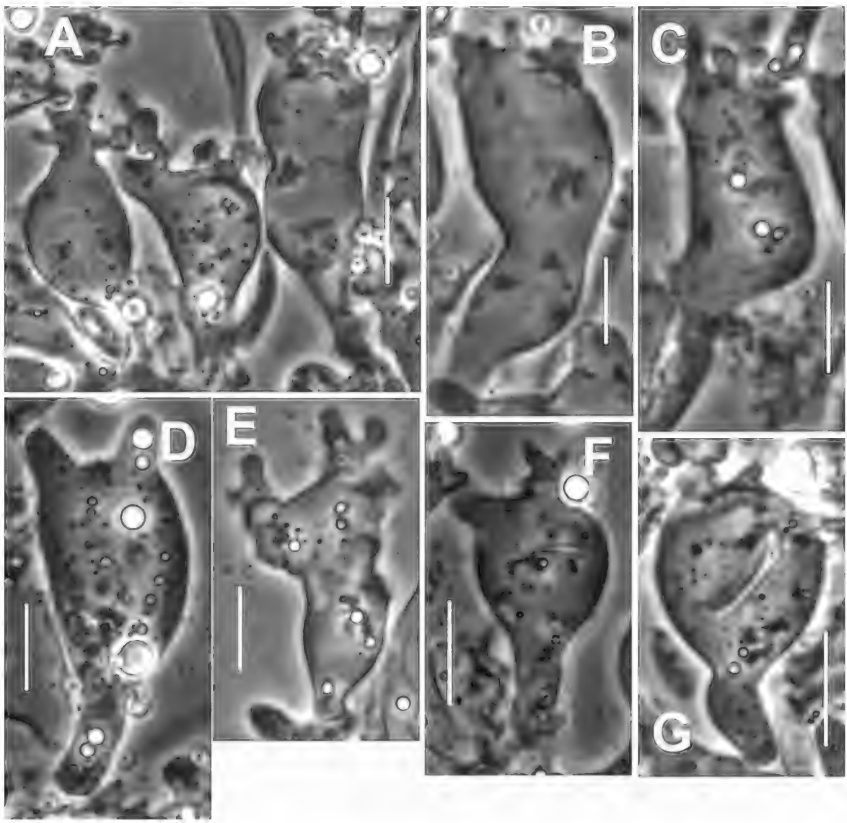


Fig. 47. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Cheilocystidia. A. Cluster of three cheilocystidia; B, C, E-G. Cheilocystidia with distal prong-like ornamentation; D. Cheilocystidium with two simple sterigmatoid apical lobes. Scale bars = 10 µm.

clavate to keg-shaped, always ornamented with scattered stripes or annular appearance; 3) slender hyphae (Fig. 44B-D), 2.5–4.5 µm diam., firm-walled, often meandering, usually delicately ornamented with spiculate deposits, appearing dense (PhC); and 5) rare cheilocystidium-shaped individuals, 34–46 × 5–7.5 µm, appearing to arise below the subpellis and permeate the pileus surface, clavate, stalked, thick-walled (wall <1.5 µm thick, hyaline) distally pronged to coarsely divided with apical prongs. Pleurocystidia (Fig. 45) abundant, 35–45 × 5–8 µm, slender-fusiform to fusiform, hardly discernable from basidioles when immature, conspicuously clamped;

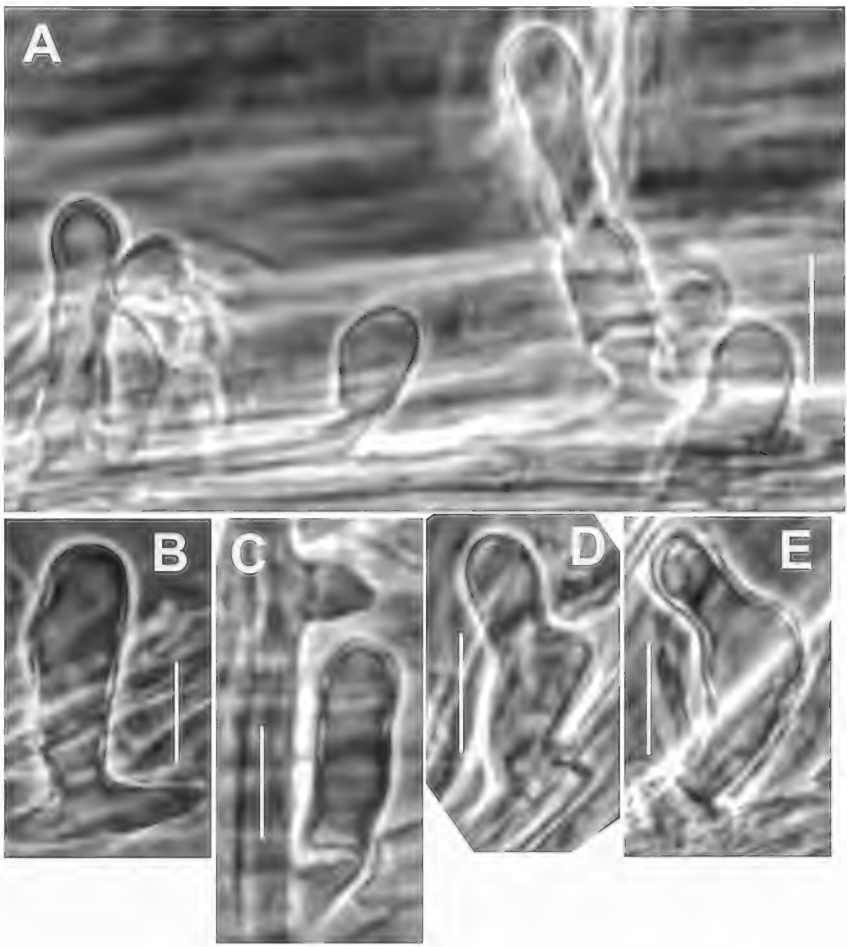


Fig. 48. *Collybiopsis minor*. (TFB 11930; TENN–F-059993). Upper stipe caulocystidia. A. Survey. B-E. Individual caulocystidia. Scale bars = 10 μm.

contents multiguttulate by maturity. Basidioles (Fig. 46A) 30-37 × 7-9 μm (at widest point), clavate, subcapitulate, clamped; contents multiguttulate; basidia (Fig. 46B-D) 30–43 × 7–9 μm, clavate, hardly subcapitulate, 4-sterigmate, clamped; contents mottled, hardly guttulate (not refringent). Basidiospores (Fig. 27) 9–10(–11) × 4–4.5 μm (E = 2.00–2.75; E^m = 2.22; L^m = 9.75 μm), ellipsoid, flattened adaxially, hardly tapered proximally,

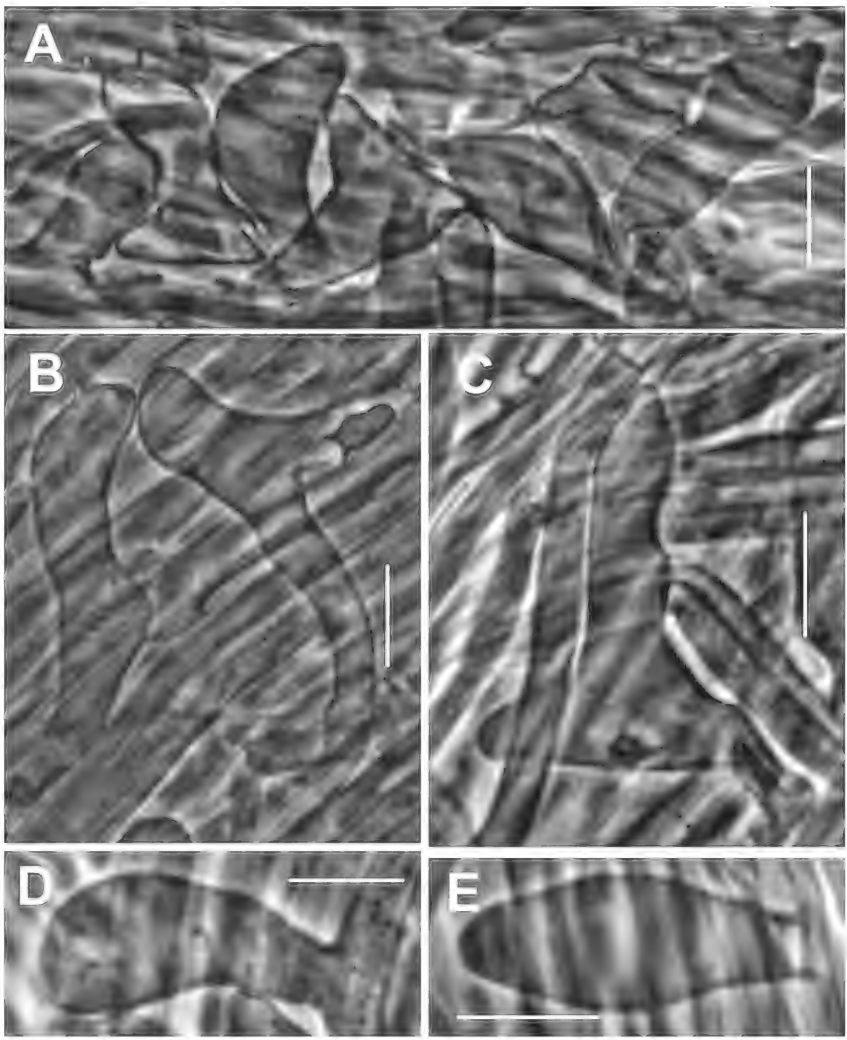


Fig. 49. *Collybiopsis minor*. (TFB 11930; TENN-F-059993). Lower stipe caulocystidia. A. Survey. B-E. Individual caulocystidia. Scale bars = 10 μm.

smooth, thin-walled, inamyloid. Cheilocystidia (Fig. 47) plentiful at lamellar edge, broadly clavate to ventricose-rostrate, firm- to thick-walled (wall <0.5 μm thick, hyaline), 30–55 × 12–20 μm (at widest point); stalk 15–25 × 3.5–5.5 μm, obscurely clamped (easily disarticulated); distal

inflated portion subglobose to broadly clavate, ranging from simply lobed (Fig. 47D) to beset with several prong-like protuberances; contents usually multiguttulate (guttules scattered, usually small, refringent PhC). Upper stipe medulla with no evidence of slime or gelatinization; medullary hyphae strictly parallel, of two types: 1) 4–8 µm diam., thick-walled (wall <1.5 µm thick, hyaline), occasionally clamped; 2) 2–3.5 µm diam., thick-walled (wall <0.7 µm thick, hyaline), sometimes meandering, occasionally clamped. Upper stipe cortex similar, weakly pigmented (straw-colored), producing caulocystidia as side branches; caulocystidia (Fig. 48) 5–35 × 4–10 µm (at widest point), papillate, digitate, cylindrical, often swollen at base, not separated from parent hypha by a septum, thick-walled (wall <1.5 µm thick, hyaline). Lower stipe medulla with no evidence of slime or gelatinization; medullary hyphae free (not in slime matrix), strictly parallel, of two types: 1) 3.5–8 µm diam, firm- to thick-walled (wall <0.7 µm thick, hyaline), occasionally clamped; and 2) 2–3.5 µm diam, appearing dense (PhC), frequently clamped, often branched and with "H"-connections. Lower stipe cortex weakly pigmented (straw-colored); cortical cells 3–4.5 µm diam, thick-walled (wall <0.7 µm thick), producing caulocystidia (Fig. 49) as side branches; caulocystidia ranging from broadly fusiform (Fig. 49D, E) to stalked and coarsely lobed (Fig. 49A-C) and inflated <14 µm broad, thick-walled (wall <0.7 µm thick, hyaline), obscurely clamped. Stipe cortex ochraceous-red-brown in IKI + BF.

Commentary: The holotype collection (about 25 basidiomata), originally identified as *Marasmiellus ramealis*, was later revised to *Ma. stenophyllus*. In reality, the pileipellis lacks any *Rameales*-structure, and tramal tissues are devoid of any slime or gelatinous deposition. Similar (but apparently unrelated) are *Marasmiellus synodicus* (Kunze ex Fr.) Singer, a European taxon, and *Marasmius subsynodicus* Murrill, which differs by fruiting on chips and sticks of *Pinus*, distant lamellae, greenish yellow pileus, smaller spores (4–5 × 2 µm, teste Murrill), and more southern distribution. Phylogenetically, *Ma. stenophyllus* appears as sister to a yet-unnamed taxon (MW386874) and more broadly to *Co. quercophila* and *Co. melanopus*.

Additional specimens examined: **USA, North Carolina, Jackson Co.**, vic. Cashiers, trail to Panthertown Valley from Bald Rock, 13.VIII.1993, coll. Nadya Psurtseva & RHP, TFB 10358 (TENN-F-057197). **South Carolina, Oconee Co.**, Walhalla Fish Hatchery, trail to Ellicott Rock, 34°52′58″N 83°20′58″W, 29.VII.1993, coll. RHP, TFB 6284 (TENN-F-052933); Burrell's Ford Campground, 34°52′58″N 83°20′58″W, 12.VIII.2014, coll. HBS class, TFB 14516 (TENN-F-069211).

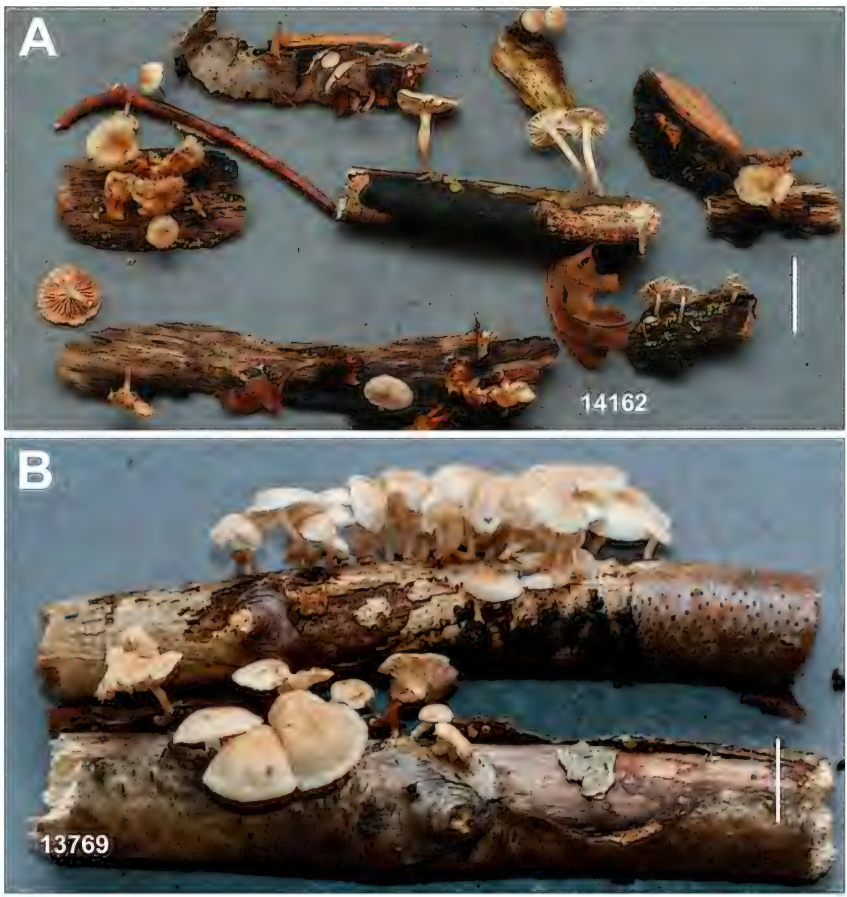


Fig. 50. *Collybiopsis ramealis*. Basidiomata.
A. (TFB 14162; TENN-F-067913). B. (TFB 13769; TENN-F-065145). Scale bars = 10 mm.

Collybiopsis ramealis (Bull.) Millsp.,
West Virginia Geol. Surv. Pt. 1: 127. 1913. Figs 50–60

≡ *Agaricus ramealis* Bull., Herb. France 7: tab no. 336 1788, nom. sanct.

Neotype (designated by Antonín & Noordeloos 1993): France, dept. Pas de Calais, Boulogne sur Mer, 14.X.19873, ME Noordeloos 7310, L.

Epitype (**hic designatus, IF 556205.**): Belgium, Couvin, Damon, Ardennes Mts., River de Rome, 50°01.45′N 4°32.21′W, 8.IX.2010, coll. A Methven, TFB 13769 (TENN-F-065145).

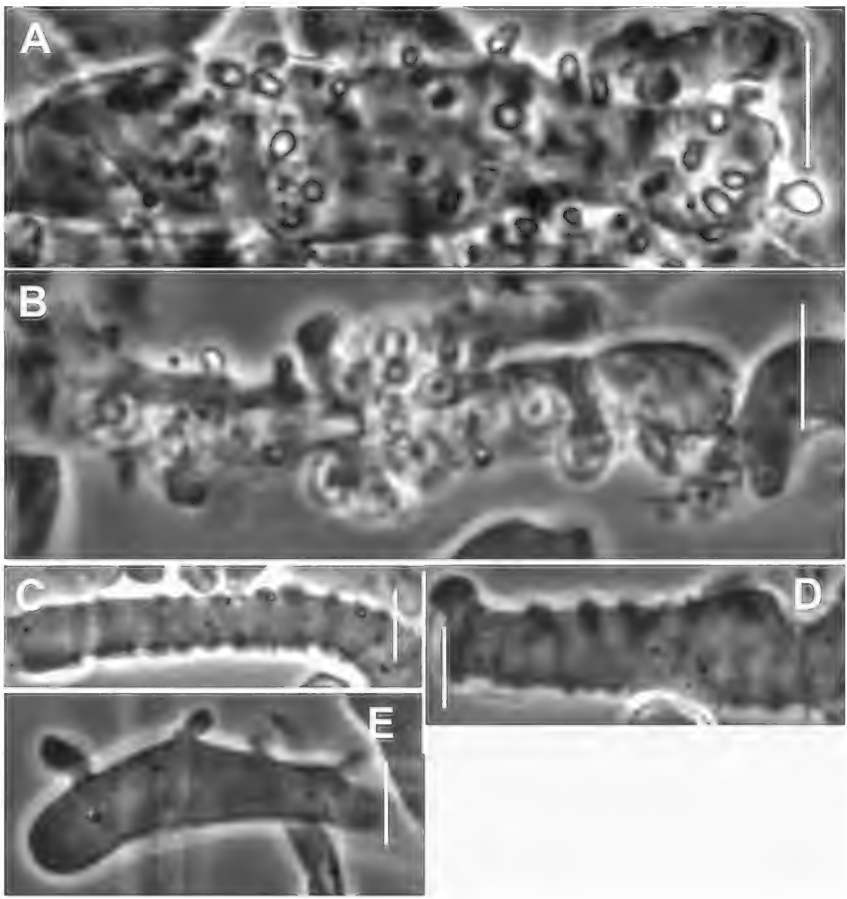


Fig. 51. *Collybiopsis ramealis*. (TFB 14546; TENN-F-069241). Pileipellis elements. A, B, E. Diverticulate hyphae. C, D. Ornamented hyphae. Scale bars = 10 μm.

Basidiomata (Fig. 50) diminutive, gregarious to densely gregarious, occasionally in troops, drying to "ochraceous buff" 5A5 to "wood brown" 7C4. Pileus 3–15 mm broad, matt, shallowly convex to applanate with involute margin, occasionally abruptly umbonate, never umbilicate but irregularly pulvinate, minimally striate at margin, not hygrophanous; disc off-white, "cream buff" 4A4, "light pinkish cinnamon" 7A2, "cinnamon buff" 6B4 to "sayal brown" 6C5, light brown 6D5-6, or paler when young 6D4,"vinaceous buff" 9B2, outward "pinkish buff" 6A3, "pale pinkish cinnamon" 6A2,

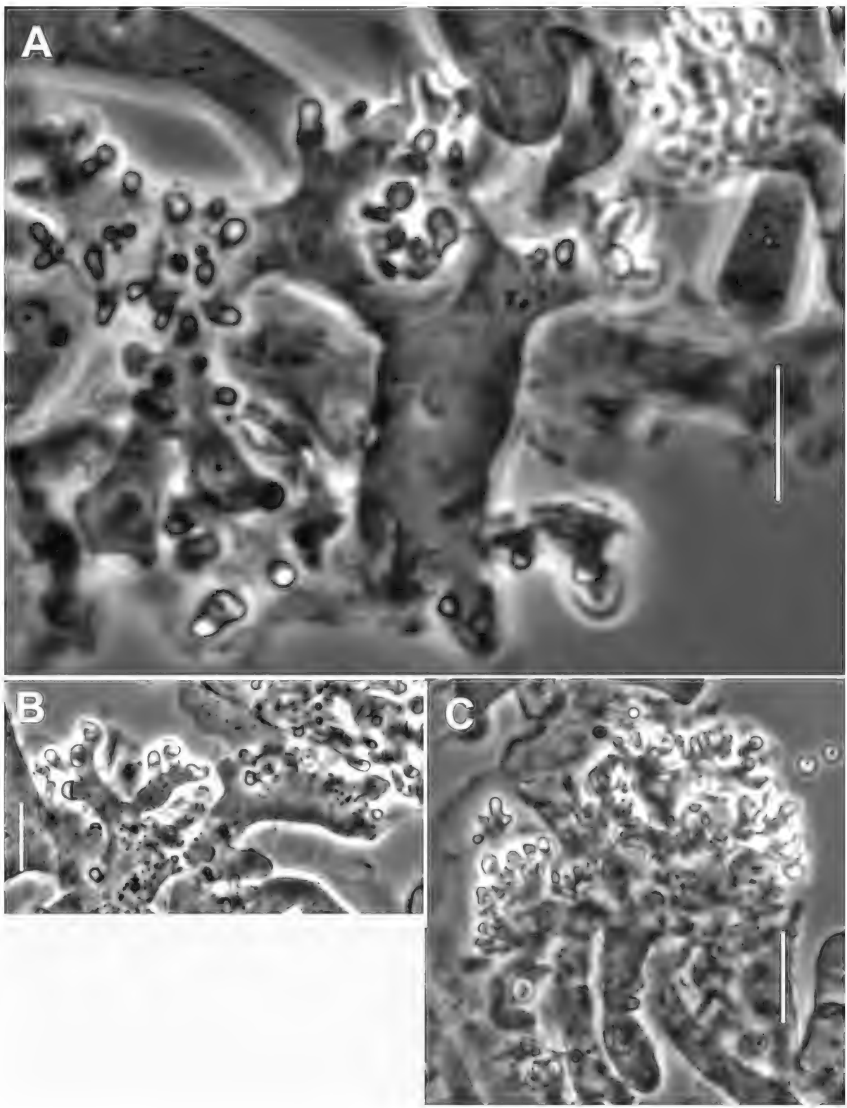


Fig. 52. *Collybiopsis ramealis*. (TFB 14546; TENN-F-069241).
Pileipellis elements; diverticulate hyphal termini. Scale bars = 10 µm.

"pale pinkish buff" 6A2 to "tilleul buff" 7B2, sometimes yellowing in age (orange white 5A2 disc, margin 4A2). Lamellae subdecurrent (and then ending abruptly on stipe), adnexed to adnate to appearing free, more or

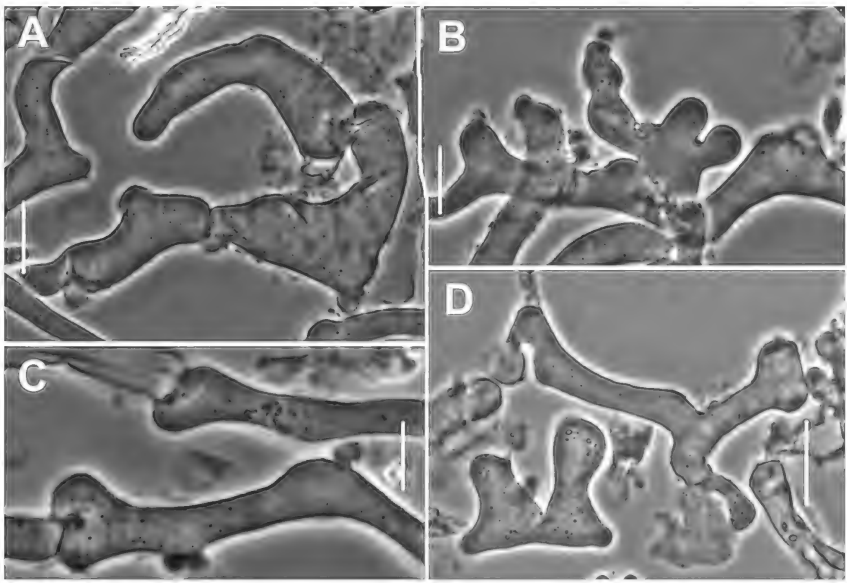


Fig. 53. *Collybiopsis ramealis*. (TFB 14546; TENN-F-069241). Inflated subpellis hyphae. Note prominent clamp connections. Scale bars = 10 μm.

less arcuate, not ventricose, seceding slightly when dried to appear free or pseudocollariate, 0.7-1 mm broad, distant, subdistant to close, (L + ll = 40–43, L = 11–14), thickish, usually concolorous with pileus surface, off-white to "pale pinkish buff" 6A2, "warm buff" 5A4, "pale pinkish cinnamon" 6A2, "pinkish buff" 6A2 with white edge, occasionally suffusing to "light pinkish cinnamon" 7A2 sometimes yellowing in age to "cartridge buff" 30A2 and tending toward crisping in older basidiomata; buttressing rare; anastomosis absent. In normal pilei, hymenophore taking on a fleshy necropigment upon drying. Stipe 6–20 × 1–2 mm broad at apex, equal and remaining so or tapering downward to 0.5-0.8 mm broad at base, inflated apically, there "pale pinkish cinnamon" 6A2, to concolorous with lamellae and minutely flocculose, downward "cream buff" 4A4, "sayal brown" 6C5, "cinnamon buff" 6D4, "vinaceous buff" 9B2, "pinkish cinnamon" 7B5, to "clay color" 5C6, at base "cinnamon buff" 6D4 or "wood brown" 7C4, sometimes yellowing 4A2, "yellow ocher" (orange-white 5A2) and then suffusing light brown 6D4 to brownish orange 6C7, in age occasionally suffusing fleshy cream to "Pompeian red" 10C6 toward base, smooth, without basal pad.

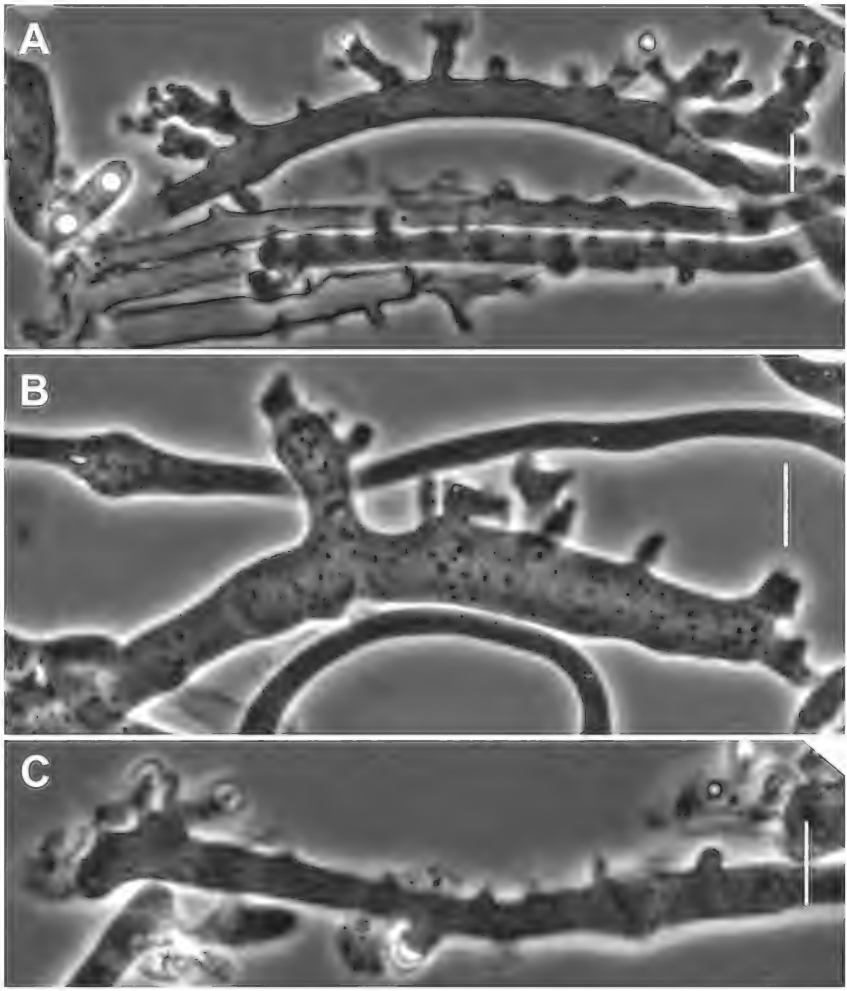


Fig. 54. *Collybiopsis ramealis*. (TFB 14163; TENN-F-067913).
Lamellar trama; diverticulate hyphae. Scale bars = 10 µm.

Odor sometimes weakly of garlic or fresh but otherwise negligible; taste not distinctive.

Habitat & phenology: Hardwood (at least *Fagus* or *Quercus*), occasionally on *Rubus* canes, *Crataegus* or other woody substrates, rotting wood, branches, twigs and bark; Europe including Scandinavia and Caucasus; late Summer, early Autumn.

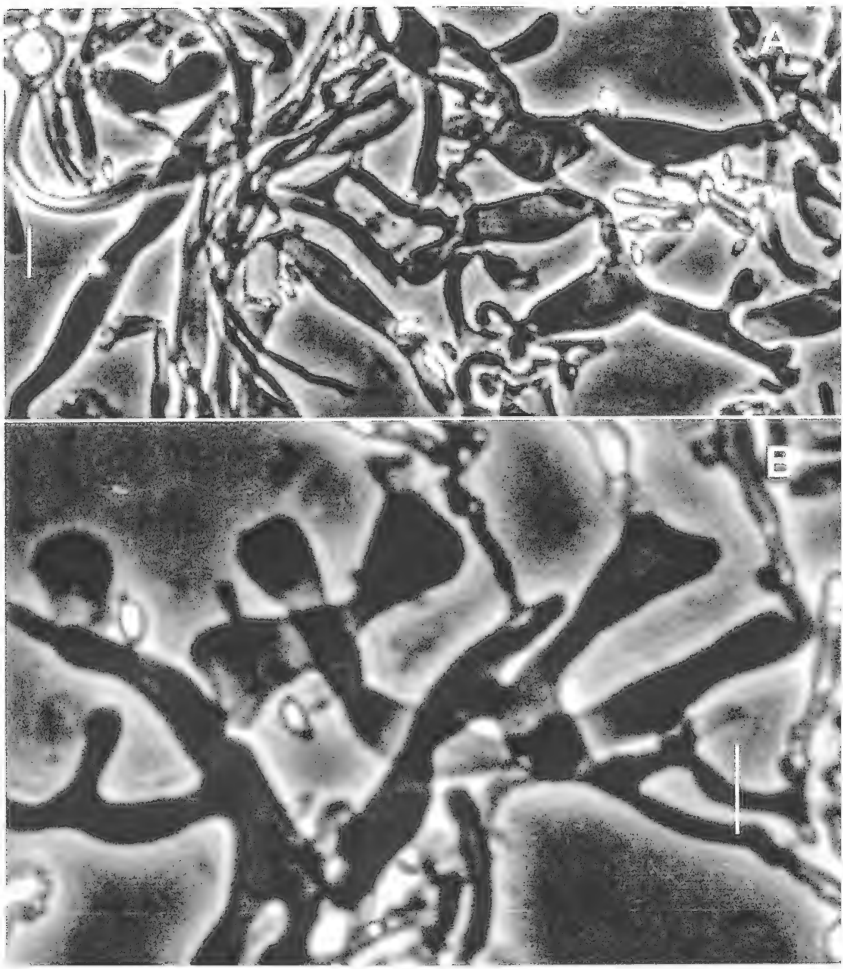


Fig. 55. *Collybiopsis ramealis*. (TFB 14573; TENN-F-069270).
Lamellar trama; inflated hyphal segments and termini. Scale bars = 10 µm.

Pileipellis constructed of the following elements: 1) erect filamentous hyphae emerging from subpellis, 25–50 × 4–5 µm, equal to subtly subcapitulate, hyaline, firm-walled, arising as side branches from repent hyphae; 2) antler-shaped hyphae 3–7(–10) µm diam, branched more or less at right angles, often ending in short, blunt, divaricate spurs (tibiiform; *Rameales*-structure; Fig. 51A, B); 3) as above but distinctly ornamented in

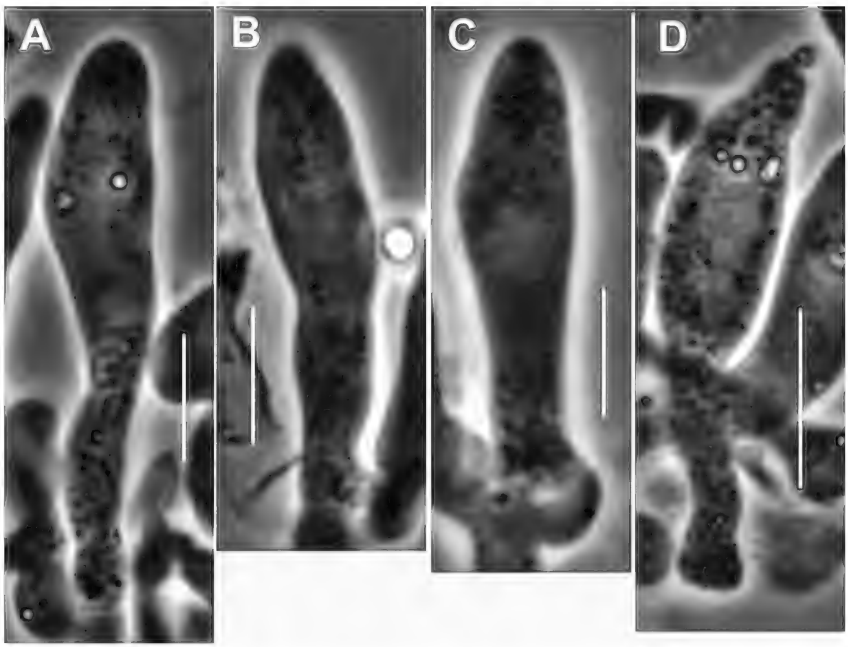


Fig. 56. *Collybiopsis ramealis*. (TFB 14546; TENN-F-069241). Pleurocystidia. Note prominent clamp connection in C. Scale bars = 10 µm.

annular or striped configuration (Fig. 51C, D), always in short lengths; 4) repent hyphae 4–8 µm diam, beset with closely scattered thumb shaped to digitate setulae 1–4 × 0.7–1.0 µm, (Fig. 52B, E) apparently as interseptal hyphal lengths and also as hyphal termini, and then more or less broom cell-like shapes (Fig. 52); setulae as above, often with refringent tips (PhC). Subpellis hyphae loosely interwoven without evidence of slime matrix or sheath, 3.5–15 µm diam (Fig. 53), thin- to firm-walled, conspicuously clamped. Pileipellis near pileus margin a coarse *Rameales*-structure, setulae coarser, knobby, not papillate, closely scattered. Lamellar trama loosely interwoven; hyphae include scattered diverticulate (Fig. 54) and antler-shaped divaricate elements (Fig. 55). Pleurocystidia (Fig. 56) 24–33 × 6–7.5 µm, common to scattered but not normally abundant, digitate (and then difficult to distinguish from basidioles) to narrowly fusiform, conspicuously clamped; contents heterogeneous with scattered granules and often 1–2 refringent inclusions (PhC). Basidioles (Fig. 57A)

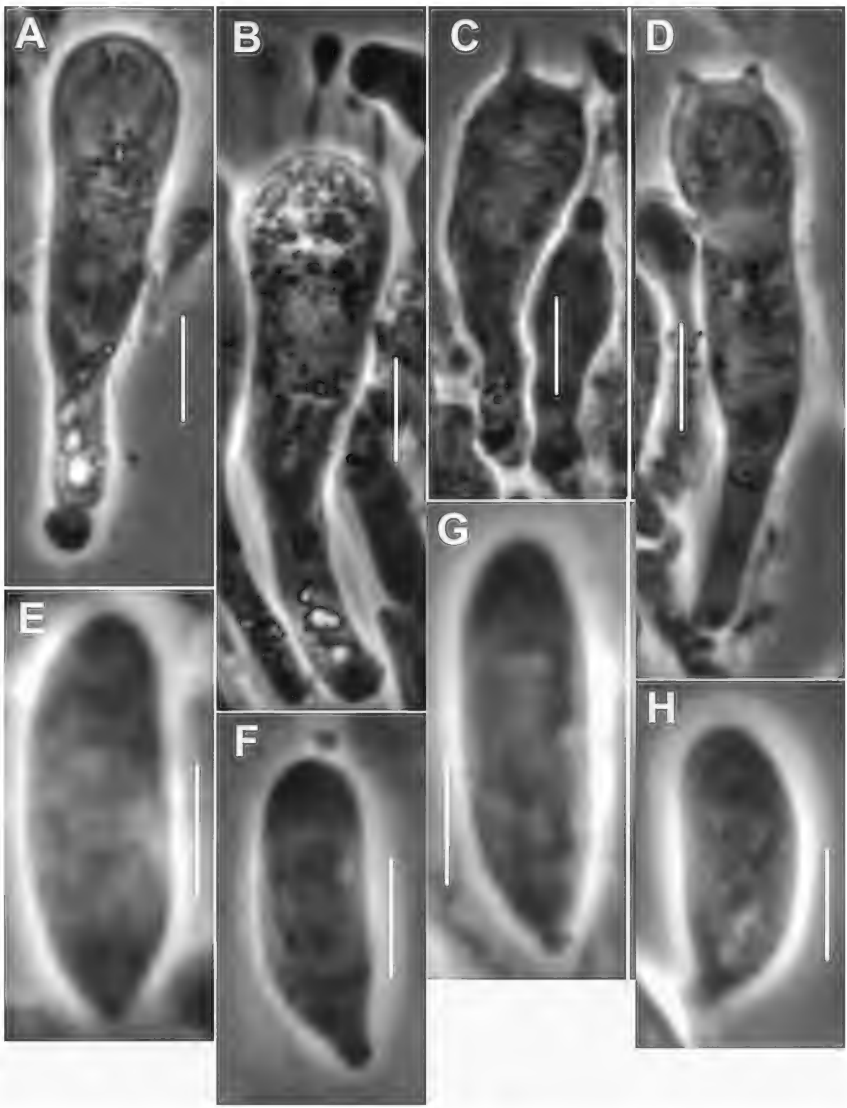


Fig. 57. *Collybiopsis ramealis*. (TFB 13755; TENN-F-065145).
A. Basidiole. B-D. Basidia. E-H. Basidiospores. Scale bars: A–D = 10 µm, E-H = 5 µm.

clavate to subcapitulate. Basidia (Fig. 57B-D) 26–32 × 7–8.5 µm, clavate to subtly subcapitulate, 4-sterigmate (sterigmata very slender, easily collapsed), conspicuously clamped; contents heterogeneous with scattered

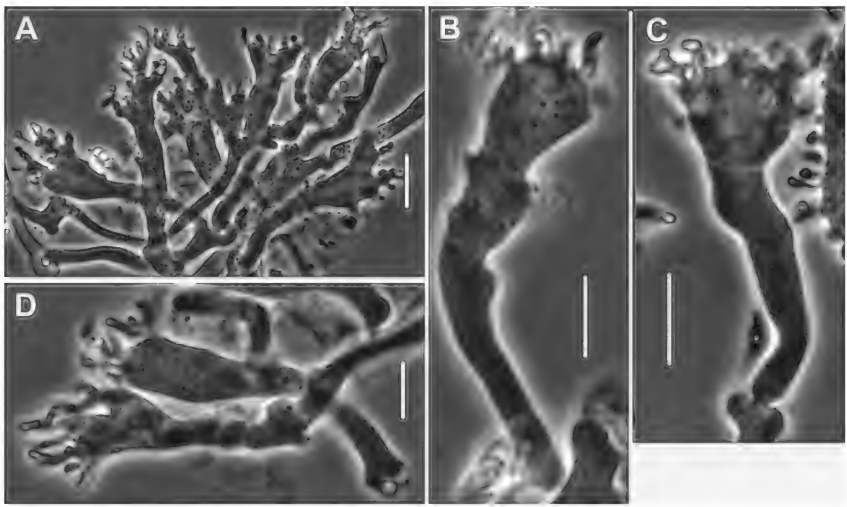


Fig. 58. *Collybiopsis ramealis*. (TFB 14573; TENN-F-069270). Clavate cheilocystidia. Scale bars = 10 µm.

granules. Basidiospores (Fig. 57E-H) (6–)7–10(–11.5) × 2.5–4(–4.5) µm (E= 1.76–3.20; E^m = 2.39; L^m = 8.61 µm), slender ellipsoid, marasmioid (tapered proximally), thin-walled, inamyloid; contents 2–3-guttulate to minutely heterogeneous, appearing foamy. Cheilocystidia (Figs. 58–60) (27–)50–84 × 12–22 µm (at widest point), thickly scattered, often appearing as pseudocystidia (i.e. arising in subhymenium, not in hymenium), ranging from clavate (Fig. 58) to typically long ventricose-rostrate to spheropedunculate with apical setulae (Fig. 59, 60), but occasionally misshapen (Fig. 60), thin- to firm-walled; inflated distal portion pigmented (dark ochraceous, PhC); apical outgrowths ranging from papillate to tentacular/coralloid, apparently flexuous (diverticula, not setulae); stalk slender (1.5–2.5 µm diam), clamped; contents heterogeneous with scattered minute granular aspect. Occasional cheilocystidia clavate (12–15 µm broad, not ventricose-rostrate), beset with scattered papillate setulae. Stipe medullary hyphae strictly parallel, easily extruded in squash mounts, of two types: 1) 4–9 µm diam, thick-walled (wall <1 µm thick, hyaline), conspicuously clamped; and 2) 1–2.5 µm diam, thin- to firm-walled, widely clamped. Stipe cortical hyphae 3–6 µm diam, thick-walled, weakly pigmented (straw-colored PhC), often papillate on outside wall; papillae 0.5–2 × 1 µm, hyaline, thick-walled. Stipe surface

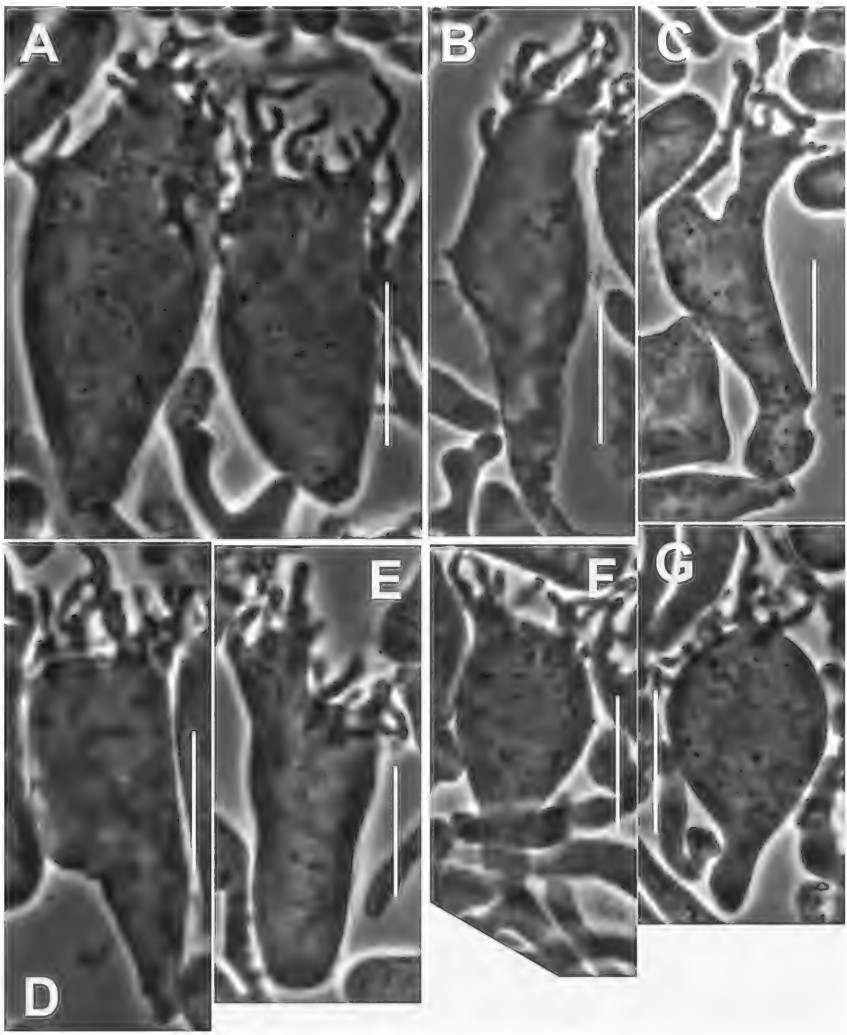


Fig. 59. *Collybiopsis ramealis*. (TFB 14573; TENN-F-069270). Ventricose-rostrate cheilocystidia. Scale bars = 10 µm.

ornamented with utriform to lobate cells arising as thin-walled termini of surface cortical hyphae, 5–10 µm diam. Upper stipe clothed in the following: 1) typical hymenium of basidia, basidioles and occasional pleurocystidia; 2) relatively normal cheilocystidia, but often distorted into odd shapes; and 3) modified cheilocystidia (distinguished by heterogeneous contents and

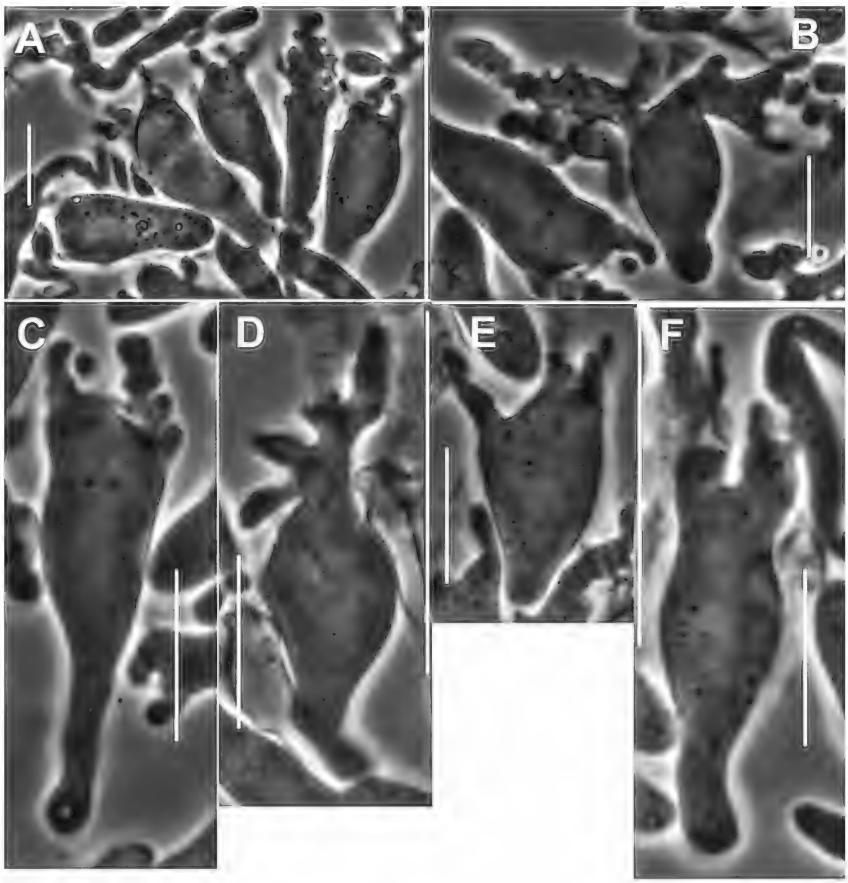


Fig. 60. *Collybiopsis ramealis*. (TFB 14546; TENN-F-069241).
Aberrant clavate cheilocystidia. Scale bars = 10 µm.

very slight pigmentation) into elongate clavate structures 9–13(–19) µm diam (at widest point), appearing as pseudocystidia, smooth to (rarely) beset with apical knobby to coralloid diverticula, firm- to thick-walled (wall <1.0 µm thick, hyaline), with basal clamp connection.

Commentary: Bulliard's illustration clearly shows decurrent, arcuate lamellae (his fig. A) perhaps seceding (his fig. B).

Cheilocystidia of all examined European specimens were pigmented. The pigment is cytoplasmic; the wall is hyaline. Contents are heterogeneous,

appearing oily with inclusions (PhC). Contents of basidioles and pleurocystidia are homogeneous but contents of mature basidia are heterogeneous, multigranular with a few small refringent guttules. Based on long pedicel stalks, cheilocystidia seem to arise deep in lamellar trama and project through the lamellar edge. This morphology has been termed "pseudocheilocystidia" (Singer 1968).

Copious spores seem to lodge on lamellar surfaces, especially at the lamellar edge. Other than the projections from cheilocystidial apices, there seems not to be a physical attraction. Spores are usually 2-guttulate; guttules polar (at proximal and distal ends of the spore), and refringent.

While the lamellar edge appears smooth at low magnification, it is delicately serrulate at 250×, with pigmented cheilocystidia appearing dark near or at the lamellar edge.

Stipes vary from terete and equal to compressed and tapering downward to a fine insertion reminiscent of that of *Marasmiellus praeacutus* (see Halling 1987).

Self-crosses were performed on collections TENN-F-052628 (Sweden), TENN-F-065120 (Belgium), TENN-F-065122 (Belgium), TENN-F-065132 (Belgium), and TENN-F-065165 (Belgium). All self-crosses showed tetrapolar mating systems. An intercollection pairing grid developed from single-basidiospore isolates from the Belgian collections showed all collections to be intercompatible, indicating that all belonged to a single mating group.

Earle's explicit assignment of *Marasmius ramealis* as type of his genus *Collybiopsis* did not constitute valid publication of the nomenclatural combination *Collybiopsis ramealis* (ICN Shenzhen Art, 36:2, see also Antonin & Noordeloos 2010: 316), although his intent was indisputable. Millspaugh (1913) made the earliest valid publication of *Collybiopsis ramealis*.

There remains a question about Earle's (1909) use of the American Code of Botanical Nomenclature (1904, 1907), of which he was a signee, especially Canon 15, embodying the "first species rule." Earle's 1909 effort was intended to be explicitly and exclusively taxonomic, not nomenclatural. In his prose summary he does not mention typification or his method of arriving at the type species of the genera in his generic summary. A search of "Tribe I. Agaricaceae §1. Gymnophylli" (Earle, pp 411-433) covering 73 genera reveals that the preponderance of genera were typified by the first (often the only) species listed in the generic protologue. But in the following, a non-first species was chosen: *Anthracophyllum*, *Leptomyces*, *Prunulus*,

Omphalina, *Pilacre*, *Lepista*, *Phylloporus*, and *Melanoleuca*. Earle's mechanical use of "The first species rule" (explicit or implicit) cannot be upheld.

But although Earle was not slavish to "the first-species rule" regarding the protologue of the various genera, he was, indeed, slavish in citing Saccardo's Sylloge Fungorum (Vol. 5, covering the agarics). In the various assemblages that Earle recognized as represented in Sylloge, Saccardo's first species do not appear to have been selected as generic types for Earle's genera.

Specimens examined: **BELGIUM**, Dimonte, vic. Hever, Jemain, Massembre, 50°09′37″N 4°51′29″E, 7.IX.2010, coll. AS Methven, TFB 13755 (TENN-F-065120); coll. S Adamčík, TFB 13745 (TENN-F-065122); vic. Heer, Bois de Baroville, vic. Beauraina, 9.IX.2010, coll. RHP, TFB 13775 (TENN-F-065151); coll. RHP, TFB 13590 (TENN-F-065165); Couvin, Damon, Ardennes Mts., River de Rome, 50°01.45′N 4°32.21′E, 8.IX.2010, coll. A Methven, TFB 13770 (TENN-F-065146). **GERMANY**, **Thuringia**, vic. Obergebra, off Rte 1016, 51°24.13′N 10°36.05′E, 30.VIII.2012, coll. RHP, TFB 14162 (TENN-F-067912); TFB 14163 (TENN-F-067913); vic. Menteroda, 51°18.18′N 10°33.52′E, 28.VIII.2012, coll. AS Methven, TFB 14140 (TENN-F-067890); Grosslohram vic Nohra, 51°24.40′N 10°36.88′E, 29.VIII.2012, coll. KWH, TFB 14150 (TENN-F-067900). **SLOVAKIA, Nitra**, Prostredny Vrich, Lovce, 48°27′04″N 18°20′49″E, 12.IX.2014, coll. RHP TFB 14573 (TENN-F-069270); Zlate Maravce Dist., vic. Hostie, 48°27′59″N 18°27′35″E, 10.IX.2014, coll A.S. Methven, TFB 14555 (TENN-F-069255); coll A.S. Methven, TFB 14546 (TENN-F-069241). **SWEDEN**, **Närke**, Hjälmarsbaden, Östra Hagen, 59°16.07′N 15°19.07′E, 10.IX.2008, coll. RHP, TFB 13520 (TENN-F-062867); **Halland**, Töto Parish, 56°54′19″N 12°47′23″E, 24.IX.1991, coll. SA Gordon, RHP, Stig Jacobsson, TFB 4727 (TENN-F-050324); **Uppland**, vic. Uppsala, Fiby Urskog, 59°52′54″N 17°21′13″E, 8.IX.1994, coll. RHP, TFB 7288 (TENN-F-053525); vic. Uppsala, 3IX.1994, coll. unknown, TFB 7248 (TENN-F-052628). **UNITED KINGDOM**, **Perthshire**, **Pitlochry**, Beach Walk along River Garry & vicinity, 56°42′16″N 3°43′47″W, 2.IX.1997, coll. RHP, TFB 6989 (TENN-F-055908).

Discussion

In future taxonomic investigations, some taxa heretofore described as *Marasmiellus* will be authoritatively sequenced and as a result, will remain securely within *Collybiopsis*. Other sequenced taxa, however, will not remain in *Collybiopsis*, with destinations (e.g., *Marasmiaceae*, *Physalacriaceae*) unpredictable. For example, taxa within *Marasmiellus* sect. *Candidi*, *Ma.* sect. *Stenophylloides*, and *Ma.* sect. *Nigripedes* (= *Tetrapyrgos*) seem destined for *Marasmiaceae* (not *Omphalotaceae-Collybiopsis*, where *Marasmiellus juniperinus* belongs). If done carefully, this process will be slow and piecemeal, inviting caution in blanket transfers.

Here it might be noted that Pegler & Young (1971) cited a specimen of *Ma. juniperinus* from Jamaica (Jamaica, Blue Mountains, 26.XII.1949,

Proctor: K). DNA sequences from this specimen might furnish a more secure (topotype) connection for the type of *Marasmiellus*.

The phylogenetic position of *Marasmiellus juniperinus* is unstable and not well-supported by either Olivera & al. (2019) or our analyses. The Olivera & al. (2019) analysis associated *Ma. juniperinus* with TENN-F-068185 (TFB14334; *Gymnopus* sp. 17) and TENN-F-068085 (TFB14228; *Gymnopus* sp.) but without support. Our current analysis associates *Ma. juniperinus* with *Co. quercophila* and *Co. melanopus*, again without support. The underlying cause is that its ITS sequence diverges from the rest of the sequenced taxa in *Collybiopsis* but does not clearly belong elsewhere based on its DNA sequences.

Despite the literature summary presented above (see Introduction), Singer's (1962) acceptance of *Marasmiellus* over *Collybiopsis* is instructive. For many years during the early 20th century an expanded concept of *Marasmius* was accepted, including numerous taxa whose micromorphology did not fully conform to the present circumscription of the genus. Kühner's (1933, 1936) treatments were especially influential. Both *Marasmiellus* and *Collybiopsis* were overlooked as candidates for atypical "*Marasmius*" taxa. In addition, they were also overlooked by some authors (notably Clements & Shear 1931, 1954) who selected type species for many genera. During these years, Singer (1938) used *Hemimycena* for a group of agarics he considered to be without a previous home. It was only later (Singer 1950) when he realized that *Marasmiellus* Murrill 1915 took priority over *Hemimycena* Singer 1938 that *Marasmiellus* came into Singer's purview. In a nomenclatural study of the genera of *Agaricales*, Donk (1962) summarized the history of *Collybiopsis* to that date. There he named a "selected" type species as *Agaricus calopus*. By 1962, Singer had accepted 59 taxa within *Marasmiellus* and, whether before or after Donk's publication, Singer also listed *Agaricus calopus* as type of *Collybiopsis*. The two authors' choice superseded Earle's explicit citation of the generic type for *Collybiopsis* (also distorting Earle's intent), thus steering *Collybiopsis* away from contention for priority over *Marasmiellus*. Both authors, however, also reported that the taxonomic concept of *A. calopus* itself was anything but secure, concluding that *A. calopus* was a "nomen dubium." Singer went one step further: if *A. calopus* was a "nomen dubium," then *Collybiopsis* was also a "nomen dubium." Singer (1962: 417-418) included *Collybiopsis* under "genera imperfectly known." We contend that *Collybiopsis* is in no way a dubious name, having been explicitly established by Earle (1909).

Acknowledgements

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Appendix I

Collybiopsis recombinations proposed

The correct name for the large clade considered here is *Collybiopsis*, which includes the type species of *Marasmiellus* (*M. juniperinus*), as well as the type species of *Gymnopus* sect. *Vestipedes* (*G. confluens*). Many epithets of appropriate binomials require transfer to *Collybiopsis*. Oliveira & al. (2019) made numerous transfers to *Marasmiellus* but, while we do not disagree with the taxonomy of these transfers, we argue that they are nomenclaturally incorrectly combined in *Marasmiellus* and not *Collybiopsis*. The list of corrected transfers below includes such species epithets with which we have experience but not those which we contend require additional investigation. Based on Fig. 1 (ITS + LSU-based phylogeny), appropriate epithets include those below, but as accurate phylogenetic placement of *Marasmiellus* and *Gymnopus* taxa (and some *Marasmius*) is determined, additional transfers will be necessary.

Collybiopsis biformis (Peck) R.H. Petersen, **comb. nov.**

IF 556182

Basionym: *Marasmius biformis* Peck, Bull. 1904 ["1903"]. N.Y. State Mus. 67: 25.

≡ *Marasmiellus biformis* (Peck) J.S. Oliveira. 2019. Mycol. Prog. 18(4): 734.

Collybiopsis brunneigracilis (Corner) R.H. Petersen, **comb. nov.**

IF 557078

Basionym: *Marasmius brunneigracilis* Corner. 1996. Nova Hedwigia, Beih. 111: 39.

≡ *Gymnopus brunneigracilis* (Corner) A.W. Wilson, Desjardin, E. Horak. 2004. Sydowia 56(1): 171.

≡ *Marasmiellus brunneigracilis* (Corner) J.S. Oliveira. 2019. Mycol. Prog. 18(5): 734.

Collybiopsis confluens (Pers.) R.H. Petersen, **comb. nov.**

IF 556183

Basionym: *Agaricus confluens* Pers. 1796. Observ. Mycol. 1: 8.

≡ *Marasmiellus confluens* (Pers.) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis dichroa (Berk. & M.A. Curtis) R.H. Petersen, **comb. nov.**

IF 556184

Basionym: *Marasmius dichrous* Berk. & M.A. Curtis. 1853. Ann. Mag. Nat. Hist. 2 12: 426.

≡ *Marasmiellus dichrous* (Berk. & M.A. Curtis) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis diminuta (Berk. & Broome) R.H. Petersen, **comb. nov.**

IF 56185

Basionym: *Agaricus diminutus* Berk. & Broome. 1871. J. Linn. Soc., Bot. 11: 251.

Collybiopsis disjuncta (R.H. Petersen & K.W. Hughes) **comb. nov.**

IF 556777

Basionym: *Gymnopus disjunctus* R.H. Petersen & K.W. Hughes. 2014. N. Am. Fung. 9: 2.

≡ *Marasmiellus disjunctus* (R.H. Petersen & K.W. Hughes) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis eneficola (R.H. Petersen) R.H. Petersen, **comb. nov.**

IF 556186

Basionym: *Gymnopus eneficola* R.H. Petersen. 2014. Omphalina 5(5): 5.

≡ *Marasmiellus eneficola* (R.H. Petersen) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis fibrosipes (Berk. & M.A. Curtis) R.H. Petersen, **comb. nov.**

IF 557077

Basionym: *Marasmius fibrosipes* Berk. & M.A. Curtis. 1869. J. Linn. Soc. Bot. 10: 293.

≡ *Collybia fibrosipes* (Berk. & M.W. Curtis) Dennis. 1951. Trans. Brit. Mycol. Soc. 34(4): 448

≡ *Gymnopus fibrosipes* (Berk. & M.A. Curtis) J.L. Mata. 2003 Mycotaxon 86: 315.

Collybiopsis foliiphila (A.K. Dutta, K. Acharya & Antonín) R.H. Petersen, **comb. nov.**

IF 557080

Basionym: *Marasmiellus foliiphilus* A.K. Dutta, K. Acharya & Antonín. 2015. Mycol. Prog. 14: 5.

Collybiopsis gibbosa (Corner) R.H. Petersen, **comb. nov**.

IF 556187

Basionym: *Marasmius gibbosus* Corner. 1996. Nova Hedwigia, Beih. 111: 53.

≡ *Marasmiellus gibbosus* (Corner) J.S. Oliveira. 2019. Mycol. Prog. 18: 734.

Collybiopsis indocta (Corner) R.H. Petersen, **comb. nov**.

IF 556188

Basionym: *Marasmius indoctus* Corner. 1996. Nova Hedwigia, Beih. 111: 60.

≡ *Marasmiellus indoctus* (Corner) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis juniperina (Murrill) R.H. Petersen, **comb. nov.**

IF 556189

Basionym: *Marasmiellus juniperinus* Murrill. 1915 N. Am. Fl. 9(4): 243.

Collybiopsis luxurians (Peck) R.H. Petersen, **comb. nov**.

IF 556190

Basionym: *Collybia luxurians* Peck. 1897. Bull. Torrey Bot. Club 24: 141.

≡ *Marasmiellus luxurians* (Peck) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis melanopus (A.W. Wilson, Desjardin & E. Horak) R.H. Petersen, **comb. nov.**

IF 556191

Basionym: *Gymnopus melanopus* A.W. Wilson, Desjardin & E. Horak. 2004. Sydowia 56: 181

≡ *Marasmiellus melanopus* (A.W. Wilson, Desjardin & E. Horak) J.S. Oliveira. 2019. Mycol. Prog. 18: 735

Collybiopsis menehune (Desjardin, Halling & Hemmes) R.H. Petersen, **comb. nov**.

IF 556192

Basionym: *Gymnopus menehune* Desjardin, Halling & Hemmes. 1999. Mycologia 91(1): 173.

≡ *Marasmiellus menehune* (Desjardin, Halling & Hemmes) J.S. Oliveira. 2019. Mycol. Prog. 18: 375.

Collybiopsis mesoamericana (J.L. Mata) R.H. Petersen, **comb. nov**.

IF 556193

Basionym: *Gymnopus mesoamericanus* J.L. Mata. 2006. Sydowia 58(2): 283.

≡ *Marasmiellus mesoamericanus* (J.L. Mata) J.S. Oliveira. 2019. Mycol. Prog. 19: 735.

Collybiopsis micromphaloides (R.H. Petersen & K.W. Hughes) R.H. Petersen, **comb. nov.**

IF 556778

Basionym: R.H. Petersen & K.W. Hughes. 2014. N. Am. Fungi 9: 6.

≡ *Marasmiellus micromphalioides* (R.H. Petersen & K.W.Hughes) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis neotropica (Singer) R.H. Petersen, **comb. nov**.

IF 556942

Basionym: *Collybia neotropica* Singer. 1962 ["1961"]. Sydowia 15: 54.

≡ *Gymnopus neotropicus* (Singer) J.L. Mata. 2003. Mycotaxon 86:313.

≡ *Marasmiellus neotropicus* (Singer) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis nonnulla (Corner) R.H. Petersen, **comb. nov**.

IF 556194

Basionym: *Marasmius nonnullus* Corner. 1996, Nova Hedwigia, Beih. 111: 76.

≡ *Marasmiellus nonnullus* (Corner) J.S. Oliveira 2019, Mycol. Prog. 18: 735.

Collybiopsis obscuroides (Antonín & Legon) R.H. Petersen, **comb. nov.**

IF 556943

Basionym: *Gymnopus obscuroides* Antonín & Legon. 2008. Czech Mycol. 60: 14.

Collybiopsis parvula (J.L. Mata, R.H. Petersen & K.W. Hughes) R.H. Petersen, **comb. nov**.

IF 556779

Basionym: *Gymnopus parvulus* J.L. Mata, R.H. Petersen & K.W. Hughes. 2007. Sydowia 58(2): 285.

≡ *Marasmiellus parvulus* (J.L. Mata, R.H. Petersen & K.W. Hughes) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis peronata (Bolton) R.H. Petersen, **comb. nov**.

IF 556195

Basionym: *Agaricus peronatus* Bolton. 1788. Hist. Fung. Halifax 2: 58.

≡ *Marasmiellus peronatus* (Bolton) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis polygramma (Mont.) R.H. Petersen, **comb. nov.**

IF 556944

Basionym: *Marasmius polygrammus* Montagne. 1854. Ann. Sci. Nat, Bot. ser. 4 1: 118.

≡ *Gymnopus polygrammus* (Mont.) J.L. Mata. 2003. Mycotaxon 86: 313.

≡ *Marasmiellus polygrammus* (Mont.) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis pseudoluxurians (R.H. Petersen & K.W. Hughes) R.H. Petersen, **comb. nov.**

IF 556196

Basionym: *Gymnopus pseudoluxurians* R.H. Petersen & K.W. Hughes. 2014, N. Am. Fung. 9(3): 7.

≡ *Marasmiellus pseudoluxurians* (R.H. Petersen & K.W. Hughes) J.S. Oliveira. 2019. Mycol. Prog. 19: 736

Collybiopsis quercophila (Pouzar) R.H. Petersen, **comb. nov.**

IF 556197

Basionym: *Marasmius quercophilus* Pouzar. 1982. Česka Mykol. 36(1): 1.

≡ *Marasmiellus quercophilus* (Pouzar) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis readiae (G. Stev.) R.H. Petersen, **comb. nov**.

IF 556945

Basionym: *Crinipellis readiae* G. Stev. 1964. Kew Bull. 19(1): 43.

≡ *Gymnopus readiae* (G. Stev.) J.L. Mata. 2007. Sydowia 58: 289.

Collybiopsis stenophylla (Mont.) R.H. Petersen, **comb. nov.**

IF 557079

Basionym: *Marasmius stenophyllus* Mont. 1854. Ann. Sci. Nat., Bot.Ser. 4 1: 116.

≡ *Marasmiellus stenophyllus* (Mont.) Singer. 1962. Sydowia 15: 58.

≡ *Gymnopus stenophyllus* (Mont.) J.L. Mata & R.H. Petersen. 2004. Mycoscience 45(1): 221.

Collybiopsis subcyathiformis (Murrill) R.H. Petersen, **comb. nov.**

IF 556946

Basionym: *Marasmius subcyathiformis* Murrill. 1915. N. Amer. Fl. 9(4): 269.

≡ *Marasmiellus subcyathiformis* (Murrill) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

≡ *Gymnopus subcyathiformis* (Murrill) Desjardin, Halling & Hemmes. 1999. Mycologia 91: 175.

Collybiopsis subnuda (Ellis ex Peck) R.H. Petersen, **comb. nov**.

IF 556198

Basionym: *Marasmius subnudus* Ellis ex Peck. 1898. Bull. Torrey Bot. Club 25: 287.

≡ *Marasmiellus subnudus* (Ellis ex Peck) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis subpruinosa (Murrill) R.H. Petersen, **comb. nov.**

IF 556199

Basionym: *Marasmius subpruinosus* Murrill. 1915. N. Amer. Fl. 9: 266.

≡ *Marasmiellus subpruinosus* (Murrill) J.S. Oliveira. 2019. Mycol. Prog. 18: 735.

Collybiopsis synodica (Kunze ex Fr.) R.H. Petersen, **comb. nov.**

IF 556200

Basionym: *Agaricus synodicus* Kunze ex Fr. 1830. Linnaea 5: 507.

Collybiopsis termiticola (Corner) R.H. Petersen, **comb. nov.**

IF 556201

Basionym: *Marasmius termiticola* Corner. 1996. Nova Hedwigia. Beih. 111: 101.

≡ *Marasmiellus termiticola* (Corner) J.S. Oliveira. 2019. Mycol. Prog. 18: 736.

Collybiopsis vaillantii (Pers.) R.H. Petersen, **comb. nov.**

IF 556202

Basionym: *Agaricus ericetorum* β *vaillantii* Pers. 1801. Syn. Meth. Fung. 2: 472.

Collybiopsis villosipes (Cleland) R.H. Petersen, **comb. nov.**

IF 556203

Basionym: *Marasmius villosipes* Cleland. 1934.
Toadstools Mushrooms S. Austral. 1: 166.

≡ *Marasmiellus villosipes* (Cleland) J.S. Oliveira. 2019. Mycol. Prog. 18: 736.

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Parathozetella microsperma gen. & sp. nov. from the Brazilian Amazon

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Abstract—A new genus and species of asexual ascomycete, *Parathozetella microsperma*, are described and illustrated from decaying plant material collected from three rainforest areas in Mato Grosso and Pará States. The new genus resembles *Thozetella* in sporodochial conidiomata, presence of microawns, and enteroblastic monophialidic conidiogenesis that produces lunate conidia, but *Parathozetella* can be easily distinguished by the absence of setulae.

Key words—*Ascomycota*, saprobic fungi, taxonomy, tropical fungi

Introduction

The Amazon biome, in addition to its great species richness, is also characterized by its high rate of endemism and highly diverse ecosystems

(Veríssimo & al. 2011). The fungal community found on dead and decaying forest litter is crucial for decomposing the organic matter in soil by providing energy and maintaining a nutritional balance. Among the decomposers, asexual ascomycetes are the most common fungi that decompose different plant substrates in both terrestrial (Costa & Gusmão 2016, Santos & al. 2018) and aquatic habitats (Fiuza & al. 2019, Silva & al. 2014).

Data on fungi in the Amazon currently underestimate diversity due to insufficient research (Monteiro & al. 2019, Sotão & al. 2004). Obtaining an accurate assessment of Amazonian biodiversity is further complicated by the threat to the ecosystem caused by the high rate of deforestation and resulting habitat fragmentation (Magnusson & al. 2013). Approximately 200 asexual ascomycete species have been registered in the Brazilian Amazon in the states of Pará (Castro & al. 2012, Monteiro & al. 2013, Santos & al. 2018), Amazonas (Cortez al. 2016, Fiuza & al. 2015), Amapá (Carmo & al. 2014), and Mato Grosso (Barbosa & al. 2015; 2017). Asexual ascomycetes have also been reported in the Amazon from Peru (Matsushima 1993, Zelski & al. 2014) and Ecuador (Matsushima 1993). As many Amazonian species have yet to be discovered, inventory work is encouraged and essential before we lose these precious forests due to anthropogenic factors such as habitat fragmentation and climate change. Our research team, which has focused on the Brazilian Amazon, has discovered many interesting taxa (Barbosa & al. 2015, 2017, 2019, Fiuza & al. 2015, Monteiro & al. 2013). One survey of asexual ascomycetes on plant debris in Amazonia revealed an interesting sporodochial conidioma-producing fungus with microawns and conidia but lacking setulae. While similar to *Thozetella* Kuntze, the fungus lacked the setulae that characterize this genus. Réblová & Winka (2000) demonstrated the importance of setulae in separating *Dictyochaeta* Speg. and *Codinaea* Maire, a concept supported by Seifert & al. (2011) and Li & al. (2012). Thus, we use the absence of setulae to propose a new genus for the previously undescribed fungus from the Brazilian Amazon.

Materials & methods

Expeditions were carried out to three sites at the Brazilian Amazon rainforest: Cláudia, Mato Grosso (11°34′54″S 55°17′15″W), Parque Nacional do Utinga, Belém, Pará (1°23′13″S 48°25′19″W), and Assentamento Rio Vermelho, Santa Bárbara do Pará, Pará (1°10′58″S 48°11′43″W) to collect decaying wood and petioles. Samples were placed in paper bags and taken to the laboratory at Universidade Federal de Mato Grosso (UFMT-Sinop) and Museu Paraense Emílio Goeldi, Pará for processing following Castañeda-Ruiz & al. (2016). Permanent slides were prepared in PVL resin

(polyvinyl alcohol, lactic acid, and phenol) and reproductive structures were measured and photographed under a Leica DM 500 microscope with a coupled digital camera. The holotype was deposited in the Herbario Centro-Norte Mato-Grossense, Sinop, Mato Grosso state, Brazil (CNMT), and additional materials in the Herbario João Murça Pires, Belém, Pará state, Brazil (MG). Several attempts to obtain this species in pure culture were unsuccessful.

Taxonomy

Parathozetella F.R. Barbosa, J.S. Monteiro, Fiuza, R.F. Castañeda & Gusmão, **gen. nov.**

MB 834624

Differs from *Thozetella* by the absence of setulae on conidia.

Type Species: *Parathozetella microsperma* F.R. Barbosa & al.

Etymology: Latin, *Para-* referring to similar; and *-thozetella*, referring to the genus *Thozetella*

Mycelium superficial and immersed, composed of slightly branched, septate, smooth, pale brown hyphae. Conidiomata sporodochial, superficial, scattered, brown. Conidiophores macronematous, septate, cylindrical, smooth, pale brown to brown. Conidiogenous cells enteroblastic, monophialidic, integrated, determinate, terminal, cylindrical, smooth, pale brown. Microawns mixed and immersed in the white to yellow conidial mass, smooth or verrucose at one end. Conidia lunate, septate or aseptate, smooth, asetulate, hyaline.

Parathozetella microsperma F.R. Barbosa, J.S. Monteiro, Fiuza, R.F. Castañeda & Gusmão, **sp. nov.** Fig. 1

MB 834626

Differs from *Thozetella* species by its small conidia that lack setulae.

Type: Brazil, Mato Grosso State, Cláudia, on decaying wood of lianes, 9.V.2016, coll. F.R. Barbosa (Holotype, CNMTf 81).

Etymology: Latin, *microsperma*, refers to the small size of the conidia

Mycelium superficial and immersed, hyphae, 2.5 µm diam, slightly branched, septate, smooth, pale brown. Conidiomata sporodochial, sessile, superficial, scattered, conidial mass white to yellow, 150–320 × 120–200 µm. Conidiophores macronematous, septate, cylindrical, smooth, pale brown to brown. Conidiogenous cells enteroblastic, monophialidic, integrated, determinate, terminal, cylindrical, smooth, subhyaline, 8.5–13 × 2–3 µm, with a conspicuous collarette. Microawns aseptate, uncinate, verrucose at one end, hyaline, mixed and immersed in the white to yellow conidial mass, 10–12 ×

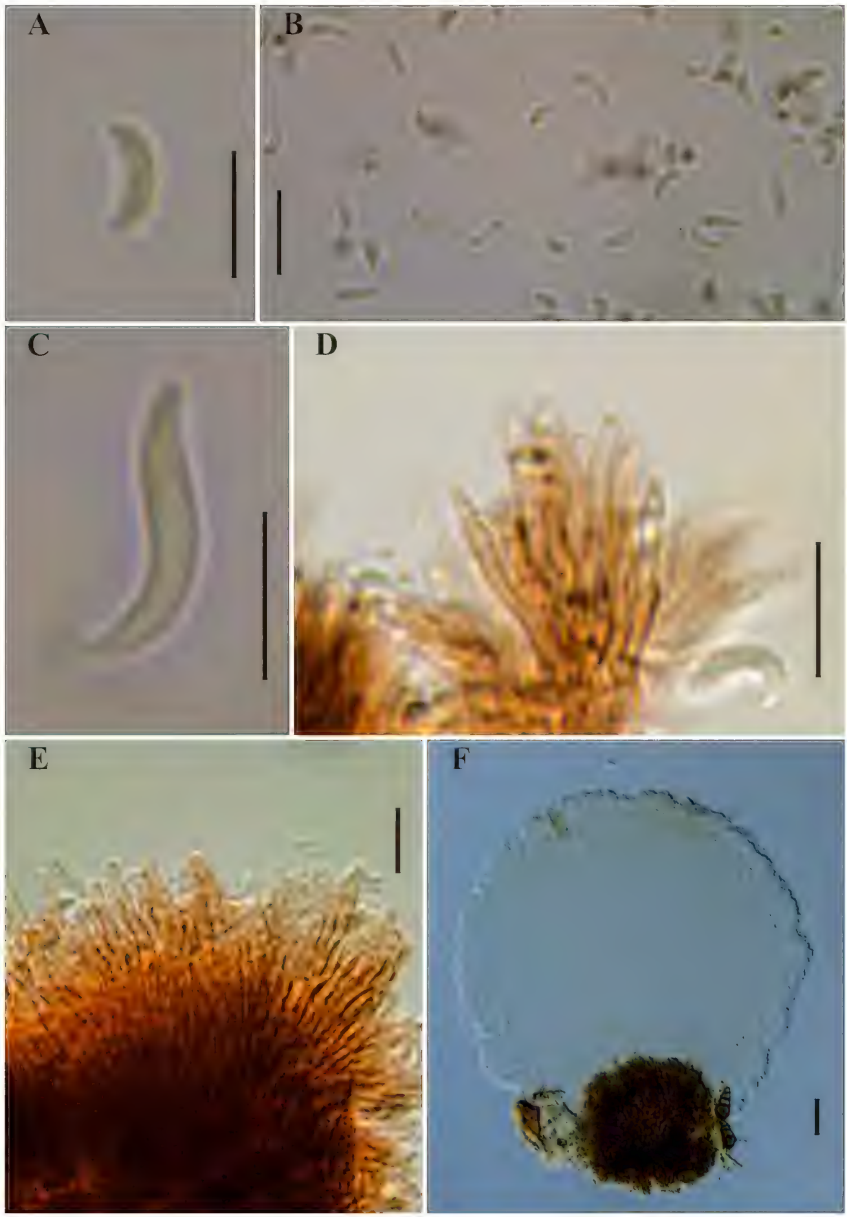

Fig. 1. *Parathozetella microsperma* (holotype, CNMTf 81). A. Conidium; B. Conidia; C. Microawn; D. Conidiogenous cells and microawn; E. Conidiogenous cells; F. Conidiomata. Scale bars: A, C = 5 µm; B, D–E = 10 µm; F = 20 µm.

1.2–1.5 µm. Conidia lunate, 0–1 septate, smooth, asetulate, hyaline, 4–5 × 1–1.5 µm. Sexual morph not observed.

Additional specimens examined–BRAZIL. Pará State: Belém, Parque Estadual do Utinga, trilha do Patuá, on decaying wood of unidentified plant: 29.IV.2019, coll. J.S. Monteiro (MG 237232). Santa Bárbara do Pará, Assentamento Rio Vermelho, on decaying petioles of *Bactris gasipaes* Kunth (*Arecaceae*), 16.V.2019, coll. A.P. Silva (MG 237239).

Comments—The production of sporodochia with monophialidic conidiogenous cells invites comparison of *Parathozetella* with some genera like *Mahabalella* B. Sutton & S.D. Patil, *Menidochium* R.F. Castañeda & W.B. Kendr., and *Minimidochium* B. Sutton. However, the presence of microawns distinguishes *Parathozetella* from those genera, placing it morphologically closer to *Thozetella*. In addition to forming conidioma (synnema and sporodochia) and microawns, however, *Thozetella* is further characterized by conidia with setulae, structures that are absent in *Parathozetella*.

We consider that production of microawns and asetulate conidia are sufficient to propose a new genus, possibly within *Chaetosphaeriaceae*, a family characterized by presence of microawns. Réblová (2000) and Réblová & Winka (2000) maintained that the presence or absence of conidial setulae was morphologically important in separating *Dictyochaeta* and *Codinaea*. Moreover, Seifert & al. (2011) and Li & al. (2012) also accepted using conidial setulae as a factor in delineating genera. Given this result we suggest establishing a new genus and species *Parathozetella microsperma* for our fungus from the Brazilian Amazon.

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Pseudosperma albobrunneum sp. nov. from coniferous forests of Pakistan

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Abstract—A new species, *Pseudosperma albobrunneum*, is described and illustrated. The specimens are from different areas of Khyber Pakhtunkhwa province, Pakistan. The identification is based on morphological characters, in combination with molecular phylogenetic analysis of sequences of the ITS region of nuclear ribosomal DNA. The species is found distinct morphologically from all closely related taxa, and molecular data confirm its novelty.

Key words—ectomycorrhizal, Himalayan, moist temperate, taxonomy

Introduction

Inocybaceae Jülich (*Basidiomycota*, *Agaricales*) is a highly diversified family of ectomycorrhizal fungi, comprising seven genera and more than 1000 species (Kobayashi 2009; Matheny & al. 2009, 2012, 2019; Kobayashi & Onishi 2010; Kropp & al. 2010; Bougher & Matheny 2011; Bougher & al. 2012; Kokkonen & Vauras 2012; Fan & Bau 2013, 2014; Braaten & al. 2014; Esteve-Raventós & al. 2015; Jabeen & al. 2016; Farooqi & al. 2017; Naseer & al. 2017; Liu & al. 2018; Ullah & al. 2018; Matheny & Kudzma 2019). The family shows more diversification in temperate regions as comparatively fewer species have been reported from tropical rain forests (Matheny & al. 2003; Matheny &

Bougher 2017). The species have demonstrated ectomycorrhizal associations with as many as 23 families of vascular plants, including low woody shrubs in arctic-alpine habitats making these fungi of high interest (Cripps & al. 2010, Matheny & al. 2019).

Among the 28 species representing different genera in *Inocybaceae* reported from Pakistan (Ahmad & al. 1997; Ilyas & al. 2013; Saba & al. 2015, 2020; Jabeen & al. 2016; Farooqi & al. 2017; Naseer & al. 2017, 2019; Liu & al. 2018; Ullah & al. 2018; Jabeen & Khalid 2020), eight represent *Pseudosperma* (Ahmad & al. 1997; Saba & al. 2015, 2020; Liu & al. 2018; Ullah & al. 2018; Jabeen & Khalid 2020).

The many classification systems proposed for the species in *Inocybaceae* include several clades, sections, subgenera, and genera based on morphological features and molecular phylogenetics (Massee 1904, Heim 1931, Kühner & Romagnesi 1953, Kuyper 1986, Singer 1986, Horak 2005, Matheny & Bougher 2006, Matheny & al. 2009, Larsson & al. 2009, Alvarado & al. 2010, Ryberg & al. 2010, Matheny & Kudzma 2019).

One multigene phylogenetic analysis by Matheny & al. (2019) recognized seven genera within *Inocybaceae,* including two new genera [*Nothocybe* Matheny & K.P.D. Latha, *Pseudosperma* Matheny & Esteve-Rav.], two subgenera elevated to generic rank [*Inosperma* (Kühner) Matheny & Esteve-Rav., *Mallocybe* (Kuyper) Matheny & al.], and three previously described genera [*Auritella* Matheny & Bougher, *Tubariomyces* Esteve-Rav. & Matheny, *Inocybe* (Fr.) Fr. sensu stricto].

Pseudosperma comprises species previously placed in *Inocybe* sect. *Rimosae* (Fr.) Quél. and characterized by cheilocystidia, absence of pleurocystidia, hyaline basidia, adnexed to sinuate lamellae, a fibrillose (rarely squamulose) and rimose pileus surface, a cylindrical stipe with a distinctly pruinose, furfuraceous, or somewhat flocculose apex, stipe context not changing color when bruised, odor often spermatic (reminiscent of green corn or honey) but occasionally nil, and smooth elliptic to (occasionally) indistinctly phaseoliform basidiospores (Matheny & al. 2019). *Pseudosperma* is represented by 70 species in Africa, Asia, Australasia, Europe, North America, and northern South America.

During field surveys for ectomycorrhizal fungi associated with *Pinaceae* in different areas of Khyber Pakhtunkhwa province, Pakistan, several collections were identified through both morphological and nrDNA ITS sequence analyses. They showed characters similar to species now classified under *Pseudosperma*. We could not find a published description that fit these

specimens nor published similar ITS sequences and propose these here as a new species

Material & methods

Samples of basidiomata were collected in four different localities in two administrative divisions of Khyber Pakhtunkhwa province, Pakistan.

Khanian is a small village in the northern Kaghan valley in the Mansehra district, Hazara division, in north-east Khyber Pakhtunkhwa province, immediately south of the main Himalayan range with a typically moist temperate climate and dominated by *Cedrus deodara* (Roxb. ex D. Don) G. Don along with *Abies pindrow* (Royle ex D. Don) Royle and *Pinus wallichiana* A.B. Jacks. (Siddiqui & al. 2013).

The Lower Dir district is located in the Hindu Kush range, Malakand division, in northwestern Khyber Pakhtunkhwa province. The area lies in the valley of the Panjkora river, which originates from the Hindu Kush ranges and joins the Swat River near Chakdara. The climate is dry temperate. *Pinus* spp. and *Quercus oblongata* D. Don [= Q. *incana* Roxb., nom. illeg.] are the dominant tree species (Champion & al. 1965). Among *Pinus*, *P. gerardiana* Wall. ex D. Don was the dominant species. Pure *Q. oblongata* forest was found in the mountain heights (H. Bashir, pers. obs.). Kalam and Mashkun, also situated in the Malakand division, are home to the offshoots of the Hindu Kush range (Hamayun & al. 2003), also dominated by *C. deodara* forests with *Pinus* spp. and *Q. oblongata* (Champion & al. 1965). These areas have a typical dry temperate climate (Stucki & Khan 1999).

Basidiomata were collected and photographed in their natural habitat. Morphological data was recorded from the fresh specimens. Color codes follow Munsell color charts (Munsell 1975). Each collection was dried using a fan heater and preserved in sealed bags. Sections from basidiomata were rehydrated in 5% KOH, stained in Congo red, and observed under a Techno MX4300H compound microscope. Microscopical characters were measured using an ocular micrometer, and drawn with the aid of a camera lucida. The abbreviation (n/m/p) represents 'n' number of basidiospores measured, 'm' number of basidiomata, and 'p' number of collections. Basidiospore dimensions were recorded as (a) b–c (d), where (a) and (d) are the extreme values, and the range b–c contains at least 90% of the calculated values; Q indicates the l/w ratio of the spores, and avQ is the average Q of all measured spores. Measurements of hyphae are given as ranges. The collections examined during this study have been deposited in the herbarium, Department of Botany, University of the Punjab, Quaid-e-Azam Campus, Lahore, Pakistan (LAH).

Genomic DNA extraction and PCR amplification of ITS1, 5.8S, and ITS2 was carried out following procedures by White & al. (1990), Gardes & Bruns (1993), and Bruns (1995). The PCR products were purified and sequenced at Macrogen Inc. (Korea). The newly generated sequences were deposited in GenBank. For phylogenetic study, consensus sequences of ITS regions were generated in the BioEdit software version 7.2.5 (Hall 1999). Sequence homology search was investigated using the BLAST algorithm at http://www.ncbi.nlm.nih.gov/. Sequences from the closest

relatives of the Pakistani species were included in the final dataset to reconstruct a phylogeny based on published phylogenies (Larsson & al. 2009, Kropp & al. 2013, Latha & Manimohan 2017, Liu & al. 2018). Sequences from *Auritella* and *Inosperma* were chosen as outgroup (Matheny & al. 2009). GenBank accession numbers are included with each taxon name in the phylogenetic tree. Multiple sequences were aligned using the webPRANK tool at https://www.ebi.ac.uk/goldman-srv/webprank/. Maximum likelihood analysis was performed in MEGA version 6 (Tamura & al. 2013) at 1000 bootstrap pseudoreplicates by finding best-fit substitution model with 1000 bootstrap replicates. The phylogeny was inferred by the Maximum Likelihood method based on the General Time Reversible model. A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.7529)).

Taxonomy

Pseudosperma albobrunneum Jabeen, Zainab, H. Bashir & Khalid, **sp. nov.**

Figs. 1, 2

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Differs from *Pseudosperma dulcamaroides* and *P. sororium* by the smaller basidiomata, white pileus becoming brownish with age, fibrillose stipe, and smooth, elongate to cylindric, sub-reniform basidiospores.

Type: Pakistan, Khyber Pakhtunkhwa, Hazara division, Mansehra district, Khanian, 2500 m a.s.l., on soil under *Cedrus deodara,* 5 August 2014, Sana Jabeen SJ102 (**Holotype** LAH35047; GenBank MG495392).

Etymology: The specific epithet refers to the white to brown basidiomata.

Pileus 1–1.8 cm in diam., conical with a prominent umbo; surface dry, rimose, fibrillose, white (10Y8/4) to brownish (7.5YR6/10); umbo yellowish (5Y8/6) becoming brownish (7.5YR6/10) at maturity; margin incurved when young. Lamellae adnexed, moderately close, up to 2 mm deep, golden brown (10YR5/6), with fimbriate edge. Stipe 5.5 × 0.4 cm, central, cylindrical, narrower towards the apex and wider towards the base; surface dry, pruinose towards apex, fibrillose; white (10Y8/4) when young, becoming grayish brown (5R4/1) to brown (7.5YR6/10) upon maturity, context off-white (5Y9/2). Odor spermatic.

Basidiospores [100/5/5] (12.7–)13.2–14.4(–16.4) × (5.3–)6.1–6.9 (–8.2) µm, avl × avw = 13.8 × 6.5 µm, Q = (1.90–)1.94–2.20(–2.50), avQ = 2.00, elongate to cylindric, constricted in the center in side view, sub-reniform, smooth, guttulate, brown in 5% KOH. Basidia (38.1–)40.3–42.2(–43.7) × (9.2–)9.5–11.8(–12.1) µm, 2–4-spored, clavate, guttulate, hyaline in 5% KOH; clamp connections observed at the base. Cheilocystidia (20.2–)25.4–27.4 (–30.3) × 4.4–6.5 µm, avl × avw = 26.4 × 5.5 µm, clavate, connected with basal

FIGURE. 1. *Pseudosperma albobrunneum*. A. LAH35288; B. LAH35047 (holotype). Scale bars = 0.5 cm. Photos by Abdul Nasir Khalid and Sana Jabeen.

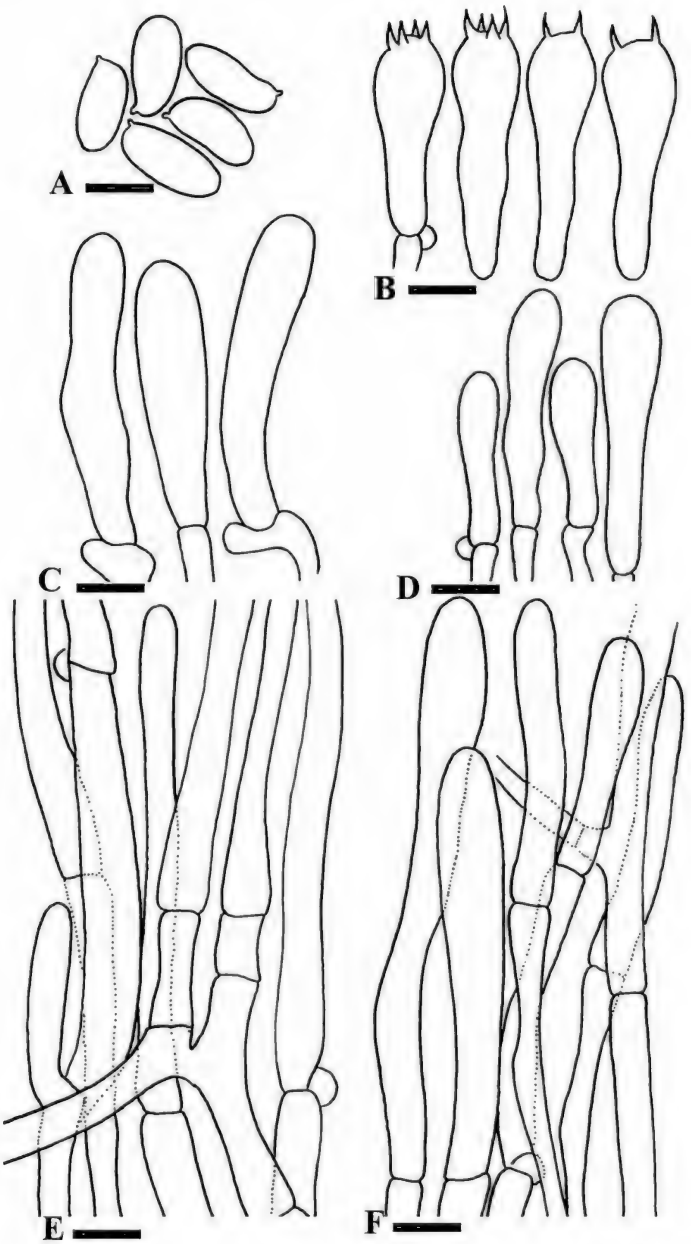

FIGURE. 2. *Pseudosperma albobrunneum* (holotype, LAH35047). A. Basidiospores; B. Basidia; C. Caulocystidia; D. Cheilocystidia, E. Pileipellis; F. Stipitipellis. Scale bars = 10 μm. Drawings by Sana Jabeen.

cell, hyaline in 5% KOH; clamp connections at base common. Pleurocystidia absent. Caulocystidia at the extreme apex of the stipe, (43.1–)45.2–50.3(–56.11) × (7.6–)9.4–10.9(–11.2) µm, avl × avw = 47.7 × 10.1 µm, clavate, hyaline in 5% KOH; clamp connections observed at the base. Pileipellis hyphae 4.6–7.7 µm wide, avw = 6.1 µm, septate, filamentous, branched, hyaline in 5% KOH; clamp connections frequent. Stipitipellis hyphae (6.1–)8.3–11.04(–11.69) µm wide, avw = 9.7 µm, septate, filamentous, rarely branched; terminal cells clavate; clamp connections observed.

Additional specimens examined: **PAKISTAN. Khyber Pakhtunkhwa, Malakand division**, Lower Dir district, near Darosh, 1840 m a.s.l., on soil under *Pinus wallichiana*, 4 September 2015, Hira Bashir & Abdul Nasir Khalid D15 (LAH35288; GenBank MG495393); Swat district, Kalam, 2400 m a.s.l., on soil under *C. deodara*, 4 September 2013, Sana Jabeen SJ146 (LAH35045; GenBank MG495395); Swat district, Mashkun, 2500 m a.s.l., on soil under *C. deodara*, 5 September 2013, Aamna Ishaq SJ147 (LAH35046; GenBank MG495396); SJ110 (LAH35289; GenBank MG495394).

Habitat & distribution—Himalayan moist *Pinaceae*-dominated forests (including *Pinus roxburghii* Sarg., *P. wallichiana,* and few *Cedrus deodara*) and dry oak-dominated temperate forests (including *Quercus oblongata*). Currently known only from Pakistan's Khyber Pakhtunkhwa province.

Ecology & distribution—1840–2500 m asl in dry and moist temperate coniferous forests, Pakistan.

Molecular phylogenetic analysis

A BLAST search of NCBI comparing the ITS consensus sequence of 658 base pairs from the type specimen of *Pseudosperma albobrunneum* (LAH35045) was closely similar to HQ604626 & KP783443 sequences named as *I. sororia* (*P. sororium* (Kauffman) Matheny & Esteve-Rav. in Index Fungorum) from USA and Russia. The ITS dataset involved 100 nucleotide sequences including these two and others closely related from the BLAST along with sequences generated during this study and those from published literature as well as those chosen as outgroup. Of the total 1642 positions in the final dataset, 771 were conserved, 465 were variable, 342 were parsimony informative, and 114 were present as singletons.

In the phylogenetic tree (Fig. 3), two major clades were recovered within *Pseudosperma* labeled as clade A and clade B. The *P. albobrunneum* sequences generated during this study formed their own lineage in clade A clustered with *P. sororium* (HQ604626 & KP783443) but separated from them with 94% boot strap support. The second set of

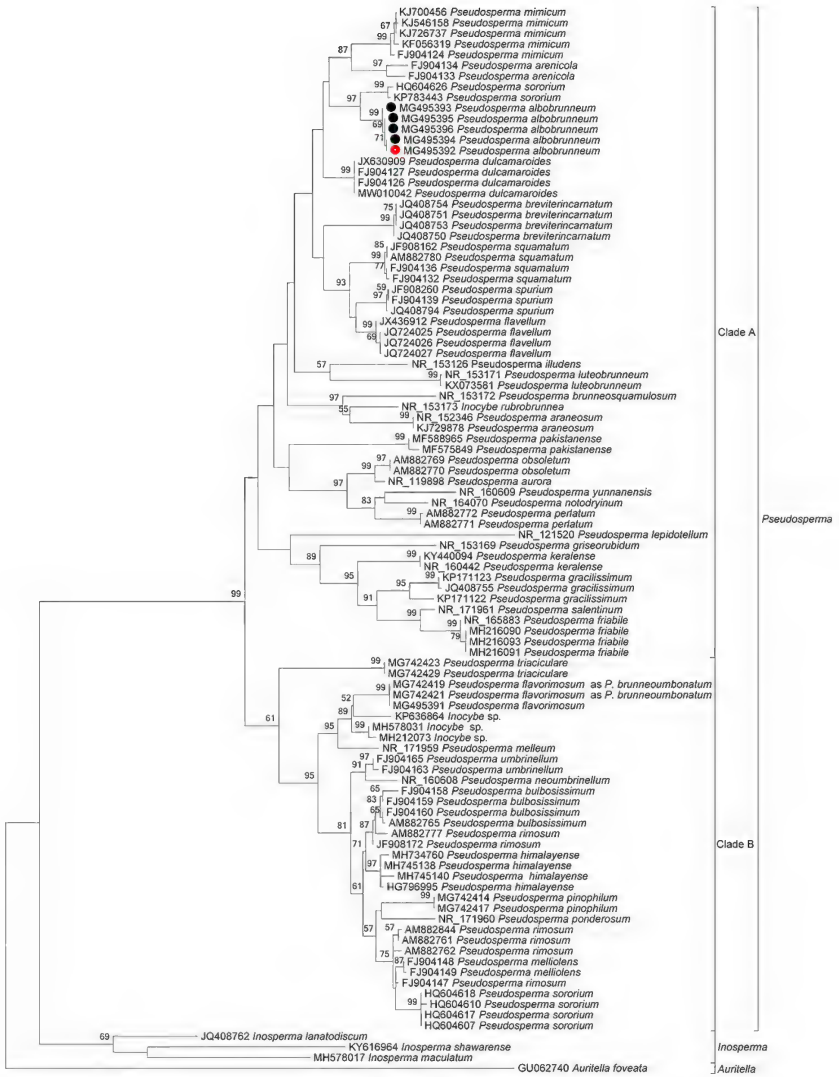

FIGURE. 3. Molecular phylogenetic analysis of *Pseudosperma albobrunneum* based on ITS sequences. Sequences generated during this study are marked with bullets; a red bullet indicates the holotype sequence.

P. sororium sequences (HQ604607, HQ604610, HQ604617, HQ604618) found in clade B does not show remarkable genetic similarity with our *P. albobrunneum* sequences.

Discussion

Pseudosperma albobrunneum is characterized by its whitish to brownish basidiomata, a very prominent long-lasting umbo, a comparatively long and slender stipe, and smooth and elongate to cylindric, sub-reniform basidiospores.

The new Pakistani species resembles the European *P. dulcamaroides* (Kühner) Matheny & Esteve-Rav., which also has brown basidiomata but with a short stipe compared with its cap diameter and with a non-umbonate pileus that becomes convex to flat at maturity (Larsson & al. 2009).

Pseudosperma sororium (Kauffman) Matheny & Esteve-Rav. showed morphological characters more or less similar to *P. albobrunneum* as described by Kauffman (1924), but its yellow pileus and basidiospores that are ellipsoid or elongate-ellipsoid and not truly sub-reniform, sub-inequilateral, obtuse at both ends distinguish *P. sororium* from *P. albobrunneum*. Furthermore, *P. sororium* has a very strong green corn odor.

In the absence of type studies, modern descriptions of *P. dulcamaroides* (Larsson & al. 2009) and *P. sororium* (as *Inocybe,* Stuntz 1978) also support *P. albobrunneum* as morphologically distinct.

Pseudosperma breviterincarnatum (D.E. Stuntz ex Kropp & al.) Matheny & Esteve-Rav. from conifer and quaking aspen forests of the western USA differs by its pinkish lamellae and brownish pileus as well as a pinkish to brownish stipe (Kropp & al. 2013).

Pseudosperma flavorimosum Jabeen & Khalid from Pakistan morphologically resembles *P. albobrunneum* but can be distinguished by its basidiospores that are elliptical, amygdaliform with broad apex and narrow base (Jabeen & Khalid 2020). In the phylogenic tree (Fig. 3), *P. albobrunneum* forms a separate clade, supporting its novelty.

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Entyloma eranthidis sp. nov. on *Eranthis longistipitata* from Uzbekistan

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Abstract—A new smut fungus, *Entyloma eranthidis* on *Eranthis longistipitata* from Uzbekistan, revealed by molecular, morphological, and ecological evidence, is described and illustrated. It differs from all other species of *Entyloma* by host specialization on *Eranthis* and by having longer (≤35(–38) µm) spores and thicker (≤10(–12) µm) spore walls. ITS rDNA sequence analysis indicates that the new species does not cluster with other species of *Entyloma* on *Ranunculaceae.*

Key words—*Entylomataceae,* phylogeny, taxonomy

Introduction

Eranthis Salisb. (*Ranunculaceae*) is a small genus with a geographic range extending from southern Europe and Turkey to central and east Asia. It contains eleven species (Rukšāns & Zetterlund 2018, Park & al. 2019). Four are with yellow perianth-segments: *E. hyemalis* (L.) Salisb. (native to South Europe), *E. cilicica* Schott & Kotschy (in the Taurus Mts and Iranian and Iraq Kurdistan; considered by some authors conspecific with previously named species; Davis & al. 1965, Tutin 1993), *E. iranica* Rukšāns & Zetterl. (from Iran), and *E. longistipitata* Regel (from central Asia) (Frizen 1993, Rukšāns & Zetterlund 2018, Park & al. 2019). The remaining species produce white

perianth-segments and have a limited distribution in the Altai-Sayan mountain region in western China or eastern Asia (Li & Tamura 2001, Park & al. 2019).

Only one smut fungus, *Urocystis eranthidis* (Pass.) Ainsw. & Sampson, is known to infect plants in *Eranthis*. This fungus is reported from Europe, Asia, North America, and Australia, with all records occurring on yellow-flowered plants: *E. hyemalis, E. cilicica,* and *E. longistipitata* (Ciferri 1938; Ainsworth & Sampson 1950; Fischer 1953; Schwarzman 1960; Vánky 1985, 2011; Scholz & Scholz 1988, 2001, 2013; Denchev 1991, 2001; Azbukina & Karatygin 1995; Scholler 1996; Vánky & Shivas 2008; Beenken & Senn-Irlet 2016; Woods & al. 2018). During an examination of fungal loans from the herbarium of University of Turku, Finland (TUR), an unidentified smut fungus on *Eranthis longistipitata* from Uzbekistan was found. Morphological and molecular studies demonstrated that it represented a new species of *Entyloma* de Bary. Its host belongs to the group of yellow-flowered species of *Eranthis.*

Entyloma is a large genus in the *Entylomataceae,* with 188 recognized species on host plants belonging to 27 families (Vánky 2011; Denchev & al. 2013; Savchenko & al. 2014, 2016; Rossman & al. 2016; Rooney-Latham & al. 2017; Savchenko & Carris 2017; Kruse & al. 2018; Kruse & Thines 2019; Richter & al. 2019). *Entyloma* species form sori in vegetative organs of plants from many different lineages of eudicots, mostly in leaves, rarely in stems, occasionally in roots, usually forming few to numerous spots, sometimes swellings or galls formed by hypertrophic growth of host tissue. The spores are permanently embedded in the host tissue, singly or in irregular groups, hyaline, yellow or yellowish brown, and usually with a smooth, two-layered wall; very rarely the outer layer is tuberculate (e.g., *E. verruculosum*) or torn apart into prismatic, pyramidal or coarse and irregular pieces (e.g., *E. urocystoides*) (Denchev & al. 2013). For many *Entyloma* species, an asexual morph is also recorded (Vánky 2011).

The importance of host specificity in delimiting species within *Entyloma* has varied significantly during the last eight decades. Savile (1947) applied a morphological species concept, based on spore sizes and asexual morph. He synonymized species with similar morphology, parasitizing host species on different genera from the same family. As a result of this broad species concept, Savile accepted only eight species of *Entyloma* on North American asteraceous hosts. Other authors (e.g. Liro 1938, Lindeberg 1959, Vánky 2011) applied narrower species concepts, considering *Entyloma* species as infecting one or more hosts from the same host genus or occasionally a few

Table 1. *Entyloma* species and GenBank accession numbers used for phylogenetic analysis

Species	Host	GenBank # (ITS)	Reference
E. arnicale	*Arnica montana*	AY854964	Boekhout & al. 2006
E. arnoseridis	*Arnoseris minima*	AY081017	Begerow & al. 2002
E. atlanticum	*Geranium tuberosum*	AY081018	Begerow & al. 2002
E. australe	*Physalis cordata*	AY081019	Begerow & al. 2002
E. belangeri	—	AY259074	Richter & al. 2019
E. bidentis	*Bidens pilosa*	AY081020	Begerow & al. 2002
E. browalliae	*Browallia americana*	AY081021	Begerow & al. 2002
E. bullosum	*Ranunculus paludosus*	MF924658	Kruse & al. 2018
E. calceolariae	*Calceolaria chelidonioides*	AY081022	Begerow & al. 2002
E. carmeli	*Eryngium falcatum*	KF310892	Savchenko & al. 2014
E. chrysosplenii	*Chrysosplenium alternifolium*	AY081024	Begerow & al. 2002
E. comaclinii	*Comaclinium montanum*	AY081025	Begerow & al. 2002
E. corydalis	*Corydalis bulbosa*	AY081027	Begerow & al. 2002
E. cosmi	*Cosmos bipinnatus*	KJ728759	Lutz & Piatek 2016
E. costaricense	*Viguiera* sp.	AY081028	Begerow & al. 2002
E. dahliae	*Dahlia* sp.	AY081029	Begerow & al. 2002
E. deliliae	*Delilia biflora*	AY081030	Begerow & al. 2002
E. davenportii	—	AY259064	Richter & al. 2019
E. diastateae	*Diastatea micrantha*	AY081031	Begerow & al. 2002
E. doebbeleri	*Dahlia imperialis*	AY081032	Begerow & al. 2002
E. eburneum	*Ranunculus repens*	MF924689	Kruse & al. 2018
E. elstari	—	AY259048	Richter & al. 2019
E. eranthidis	***Eranthis longistipitata***	**MT118137**	**this study**
E. eryngii	*Eryngium campestre*	AY081033	Begerow & al. 2002
E. eryngii-cretici	*E. creticum*	KF310894	Savchenko & al. 2014
E. eryngii-plani	*E. planum*	AY081034	Begerow & al. 2002
E. ficariae	*Ficaria verna*	MF924702	Kruse & al. 2018
E. fuscum	*Glaucium flavum*	AY081036	Begerow & al. 2002
E. gaillardianum	*Gaillardia aristata*	AY081037	Begerow & al. 2002
E. guaraniticum	*Bidens pilosa*	AY081038	Begerow & al. 2002
E. helianthi	*Helianthus annuus*	KU163607	Rooney-Latham & al. 2017
E. hieracii	*Hieracium sylvaticum*	AY081039	Begerow & al. 2002
E. holwayi	*Cosmos caudatus*	AY081040	Begerow & al. 2002
E. jolantae	*Ranunculus oreophilus*	MF924688	Kruse & al. 2018
E. klenkei	*R. marginatus*	MF924663	Kruse & al. 2018
E. kochmanii	*R. lanuginosus*	MF924678	Kruse & al. 2018

Species	Host	GenBank # (ITS)	Reference
E. lagoeciae	*Lagoecia cuminoides*	MH295129	Kruse & Thines 2019
E. linariae	*Linaria vulgaris*	AY081041	Begerow & al. 2002
E. lobeliae	*Lobelia laxiflora*	AY081042	Begerow & al. 2002
E. madiae	*Madia gracilis*	AY081043	Begerow & al. 2002
E. magocsyanum	*Tordylium cordatum*	KF310891	Savchenko & al. 2016
E. majewskii	*Ficaria verna*	MF924713	Kruse & al. 2018
E. matricariae	*Tripleurospermum perforatum*	AY081044	Begerow & al. 2002
E. microsporum	*Ranunculus repens*	MF924708	Kruse & al. 2018
E. parthenii	*Parthenium hysterophorus*	AY081026	Begerow & al. 2002
E. piepenbringiae	*Ranunculus polyanthemos* subsp. *nemorosus*	MF924664	Kruse & al. 2018
E. polysporum	*Ambrosia artemisiifolia*	AY081046	Begerow & al. 2002
E. randwijkense	—	AY259080	Richter & al. 2019
E. ranunculacearum	*Ranunculus acris*	MF924635	Kruse & al. 2018
E. ranunculi-repentis	*R. repens*	AY081047	Begerow & al. 2002
E. ranunculi-sceleratii	*R. sceleratus*	MF924672	Kruse & al. 2018
E. ranunculorum	*R. auricomus*	MF924638	Kruse & al. 2018
E. savchenkoi	*R. paludosus*	MF924675	Kruse & al. 2018
E. scandicis	*Scandix verna*	KF447773	Savchenko & al. 2016
E. serotinum	*Symphytum officinale*	AY081048	Begerow & al. 2002
E. thielii	*Ranunculus montanus*	MF924692	Kruse & al. 2018
E. verruculosum	*R. lanuginosus*	MF924651	Kruse & al. 2018
E. zinniae	*Zinnia peruviana*	AY081049	Begerow & al. 2002

closely related host genera. During the last two decades with the application of molecular methods, it became evident that members of *Entyloma* exhibit a far higher host specificity, parasitizing a single or only a few closely related host species (Begerow & al. 2002, Vánky & Lutz 2010, Savchenko & al. 2014, 2016, Kruse & al. 2018, Kruse & Thines 2019). It also became evident that much higher diversity than currently recognized in *Entyloma* should be expected (Kruse & al. 2018).

From Uzbekistan, 16 different *Entyloma* species are known, among which three are recorded on hosts in *Ranunculaceae:* the *E. ranunculi-repentis* complex on *R. polyanthemos* L., *E. thalictri* J. Schröt. on *Thalictrum minus* L., and *E. winteri* Linh. on *Delphinium biternatum* Huth (Ramazanova & al. 1987, Azbukina & Karatygin 1995).

In the present article, we describe and illustrate a new species of *Entyloma* on *Eranthis* from Uzbekistan, and analyze its phylogenetic affinities in *Entyloma*.

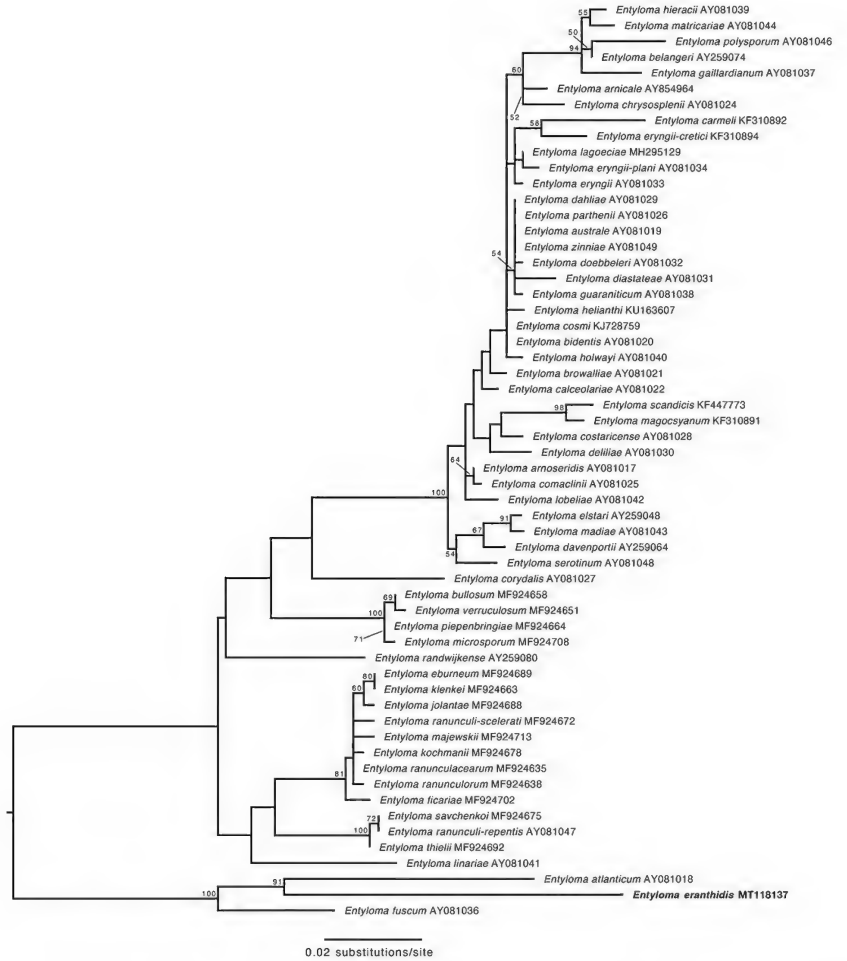

FIG. 1. Phylogenetic relationships of *Entyloma,* based on the RAxML analysis of the complete rDNA internal transcribed spacer (ITS). The new species *Entyloma eranthidis* is depicted in boldface. Bootstrap values of 1000 repetitions ≥50 are shown above branches. The phylogeny was rooted according to Begerow & al. (2002).

Materials & methods

Morphological examination

A dried specimen from the herbarium of University of Turku, Finland (TUR) was examined under light microscope (LM) and scanning electron microscope (SEM). For LM observations and measurements, spores were mounted in lactoglycerol solution

(w : la : gl = 1 : 1 : 2) on glass slides, gently heated to boiling point to rehydrate the spores, and then cooled. The measurements of spores are given as min–max (extreme values) (mean ± 1 standard deviation). For the description of the new species, a total of 300 spores from three sori (100 spores per sorus) were measured. For SEM, spores were attached to specimen holders by double-sided adhesive tape and coated with gold in an ion sputter. The surface structure of spores was observed and photographed at 10 kV accelerating voltage using a Zeiss Sigma VP scanning electron microscope. The description below is based entirely on the specimen examined.

DNA extraction, PCR amplification, and sequencing

Fragments of sori for the smut fungus and leaf tissue for the host plant were removed for DNA extraction. The samples were milled in the Fastprep-24™ Sample Preparation Instrument, using two steel beads. Genomic DNA was isolated using the my-Budget Plant DNA Kit™, according to the manufacturer's protocol 1 ("Isolation of DNA from plant material using lysis buffer SLS"). The rDNA ITS region was amplified using GoTaq™ Master Mix with primer combination ITS1-F/ITS4 (White & al. 1990, Gardes & Bruns 1993) for the smut fungus and ITS1/ITS4 (White & al. 1990) for the host plant. Standard thermal cycling conditions with annealing temperature of 52 °C were used for amplification. Five µl of PCR products were purified using ExoSAP (1:5 diluted in ddH_2O). Amplicons were sequenced in both directions with the BigDye™ Terminator Cycle Sequencing Kit V3.1 on an ABI 3130xl Genetic Analyser at the Faculty of Chemistry and Biochemistry, Ruhr University Bochum, Germany.

Phylogenetic analyses

A multiple sequence alignment of the newly generated *Entyloma* sequence and representative sequences downloaded from NCBIs GenBank (Table 1) was generated using the e-ins-i option in MAFFT v7.450 (Katoh & Standley 2013). Ambiguous positions were removed using GBLOCKS (Castresana 2000) implemented in SEAVIEW (Gouy & al. 2010). A phylogenetic tree was inferred in RAxML 8.2.11 using the GTRGAMMA nucleotide model and a rapid bootstrapping algorithm with 1000 replicates (Stamatakis 2014). The resulting phylogeny was visualized using FigTree v1.4.3 (Rambaut 2012).

Results: Phylogeny and molecular host identification

The phylogenetic analysis of the ITS data produced a topology similar to previous analyses (Begerow & al. 2002), with notable exceptions (Fig. 1). As in Begerow & al. (2002), all species of *Entyloma* on asterids, together with *E. chrysosplenii* and three species known only by their asexual morph, formed a well-supported clade, whereas those on *Ranunculales* were inferred as paraphyletic. Clades within these large groupings sometimes were incongruent with those of Begerow & al. (2002); however we note that in general our phylogeny showed limited statistical support for many clades. Nevertheless, the *Entyloma* species on *Eranthis longistipitata*

Fig. 2. *Entyloma eranthidis* on *Eranthis longistipitata* (holotype, TUR 109 345): A–C. Habit; D. Spores in LM, median view; E. Spores in LM, surface view. Scale bars: A–C = 0.5 cm; D, E = 10 µm.

formed a statistically well-supported clade with *E. atlanticum* on *Geranium tuberosum* and did not cluster together with other *Entyloma* species on *Ranunculaceae.* This clade was sister group to *E. fuscum* on *Glaucium flavum.*

The identity of the host plant, *Eranthis longistipitata,* was confirmed by ITS sequence data (now deposited in the NCBI with accession no. MT484089). The newly generated ITS sequence had a 99–100% sequence identity and 84% query coverage with the available ITS sequences of *E. longistipitata* in GenBank.

Morphology

The morphology of *Entyloma* is very simple, and differences between the species are consequently very few and vague (Lindeberg 1959). In this genus, the morphological features most commonly used for separating species are: sorus location and characteristics, spore sizes and wall characteristics, and presence of an asexual morph.

The smut fungus on *Eranthis longistipitata* from Uzbekistan is characterized by atypically well-defined morphological features, by which it can be easily distinguished from all species currently recognized in *Entyloma.* With respect to spore size, it produces by far the largest-sized spores in *Entyloma.* The only other *Entyloma* that occasionally has spores exceeding 25 µm, is *E. bullosum* (Sacc.) J. Kruse & al., with spore lengths reaching 21.5(–26.5) µm (Vánky 2011, Kruse & al. 2018). Several "*Entyloma*" species with large "spores" are referred to the *Protomycetales* (Vánky 2011). Although the smut fungus on *Eranthis longistipitata* from Uzbekistan has large spores, the morphological features and ITS sequence data clearly determine its position within *Entyloma.*

A second morphological feature distinguishing this fungus from all currently known *Entyloma* species is its spore wall, which is remarkably thick, (3.5–)4.5–10(–12) µm, with a cracked outer layer. The only other *Entyloma* that has a spore wall reaching 10 µm, is *E. martindalei* (Peck) Piątek, with the inner layer being c. 0.5 µm and the outer layer (1–)2–5 (–9.5) µm thick (Vánky 2011). For the *Entyloma* spp. parasitizing hosts in the *Ranunculales,* thick spore walls with cracked outer layer are not an uncommon morphological feature (e.g., the spore walls of *E. urocystoides* Bubák on *Corydalis solida* (L.) Clairv., *E. bullosum* on *Ranunculus paludosus* Poir., and *E. microsporum* (Unger) J. Schröt. on *Ranunculus* spp.; Denchev 2001, Vánky 2011, Kruse & al. 2018).

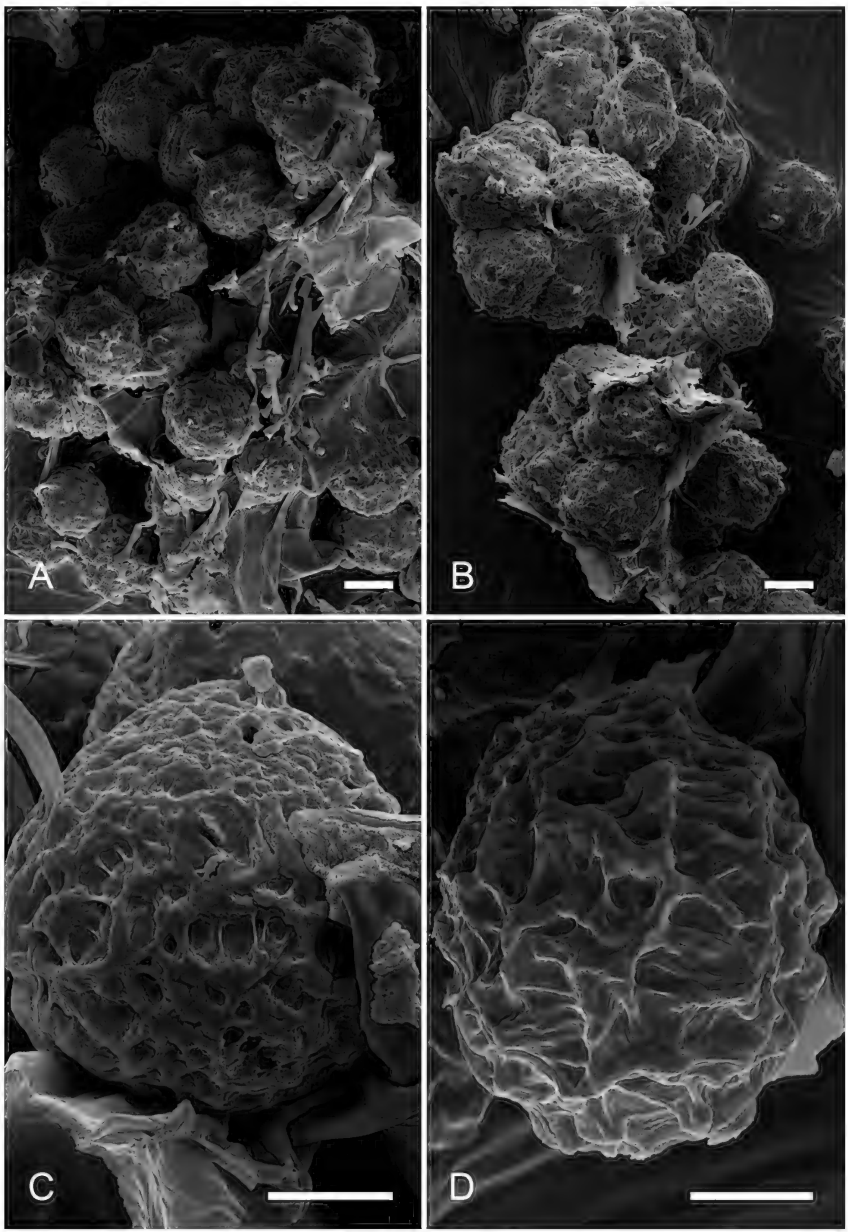

Fig. 3. *Entyloma eranthidis* on *Eranthis longistipitata* (holotype, TUR 109 345). Spores in SEM. Scale bars: A, B = 10 µm; C, D = 5 µm.

Taxonomy

Entyloma eranthidis T. Denchev, Denchev, Kemler & Begerow, **sp. nov.** FIGS 2, 3

IF 557320

Differs from the other *Entyloma* species by specialization on *Eranthis* and by having larger spores and thicker spore walls.

TYPE—on *Eranthis longistipitata:* Uzbekistan, Tashkent Region, NE of Tashkent, W Tian Shan, Ugamskii Khrebet, NE of Charvak Reservoir, 1100 m, 41°43′N 70°05′E, 1 May 1992, leg. Y. Mäkinen 92–163 (**Holotype,** TUR 109 345).

ETYMOLOGY—The epithet refers to the host genus.

SORI in leaves, forming irregularly rounded spots, 0.5–2.5 mm long, larger by fusion, amphigenous, not limited by veins, sometimes slightly protruding, reddish brown, peripherally greenish on adaxial side, clay buff on abaxial side of leaves. SPORES single, embedded in leaf tissue, usually irregular (because of the cracked surface), variable in size (18–)20–35(–38) × (16.5–)18–28(–31.5) (26.8 ± 3.3 × 23.3 ± 2.8) µm (n = 300), light to medium yellowish brown; spore wall two-layered, (3.5–)4.5–10(–12) µm thick, inner layer yellowish brown, unevenly thickened, (0.8–)1.0–3.5(–4.3) µm thick, outer layer hyaline, highly variable in thickness, (2.5–)3.5–7.5(–9.5) µm thick, initially smooth, at maturity cracking and rupturing irregularly, some ruptures reaching inner layer. As seen by SEM, outer spore wall layer very irregularly ruptured, often forming irregular ridge-like structures. ANAMORPH not seen.

COMMENTS—The immature spores of *E. eranthidis* are hyaline, with smaller sizes and a thinner, not ruptured, spore wall.

Entyloma eranthidis is known only from the type locality.

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Calogaya miniata comb. nov., *Huneckia crocina* comb. nov., and new neotropical records of *Wetmoreana brouardii*

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Abstract—New combinations *Calogaya miniata* and *Huneckia crocina* are proposed for species previously placed in *Caloplaca* s.lat., following the revised classification of *Teloschistaceae*. The taxonomy of *Wetmoreana brouardii* is discussed in relation to *Caloplaca ochraceofulva*, and its current world distribution is presented, including new records from Chile, Colombia, Peru, and Uruguay.

Key words—lichenized *Ascomycota*, nomenclature, South America, *Teloschistaceae*

Introduction

Since the publication of the new systematic arrangement of *Teloschistaceae* (Arup & al. 2013), many new genera have been proposed (e.g., Kondratyuk & al. 2014a, 2017; Søchting & al. 2014a, b; Wilk & al. 2021), with the family now comprising more than 100 genera (Kondratyuk & al. 2018). The genera are distributed among the subfamilies *Caloplacoideae*, *Teloschistoideae*, and *Xanthorioideae* (Gaya & al. 2012; Arup & al. 2013).

During an ongoing taxonomic and molecular survey on *Teloschistaceae* in Bolivia and Peru, many new discoveries were made, some already published in Wilk & Flakus (2017), Wilk (2020), and Wilk & al. (2021). In this work, two new nomenclatural combinations for species previously placed in *Caloplaca* s.lat. are proposed in *Calogaya* Arup & al., and *Huneckia* S.Y. Kondr. & al. *Calogaya* is well-delimited molecularly (Gaya & al. 2011 as "*Caloplaca saxicola* group"; Arup & al. 2013; Vondrák & al. 2016, 2018).

Huneckia is a genus recently proposed to accommodate two species, *H. pollinii* (A. Massal.) S.Y. Kondr. & al. and *H. rheinigera* (Elix & S.Y. Kondr.) S.Y. Kondr. & al., both characterized by production of an unusual, thick-walled type of ascospore (Kondratyuk & al. 2014a). *Huneckia* seems to be well-defined molecularly, morphologically, and chemically (see below for further discussion).

Current phylogenetic analyses based on three rDNA loci (ITS, nucLSU, and mtSSU) place *Caloplaca crocina*, a species producing hourglass-shaped ascospores, in *Huneckia* (*Caloplacoideae*) and *Caloplaca rouxii* in *Calogaya* (*Xanthorioideae*).

Wetmoreana brouardii is morphologically similar and often misidentified as *Caloplaca ochraceofulva* (Müll. Arg.) Jatta, for which molecular data are not yet available. Both taxa are discussed below, and the current world distribution of *W. brouardii* is presented.

Materials & methods

This study is based on the collections from the following herbaria: B, BM, E, G, KRAM, LD, M, MEL, MIN, S, and UPS. For species identification morphological characters were measured from dry material using a Nikon SMZ 1270 dissecting microscope. Anatomical characters were measured from hand-cut sections mounted in water using a Nikon Eclipse 50i light microscope. The conidia were measured based on photographs. To study the thallus anatomy of *W. brouardii* and *C. ochraceofulva* high-quality cross sections of lobes were prepared by selecting lobes which overlap other lichen thalli if possible. The granulation of anatomical structures was observed in polarized light, and solubility of granules/crystals and colour reactions were determined using 25% KOH (K) and 65% nitric acid (N). Hydrochloric acid (HCl) was used to test for the presence of calcium carbonate ($CaCO_3$) in the rocky substrate. Thallic and apothecial terminology follows Bungartz (2002) and Ryan & al. (2002, 2012). Photographic documentation was made with a Nikon DS-Fi2 digital camera combined with the imaging software NIS-Elements D v. 4.30.

The sequences used in the study were sourced from Wilk & al. (2021) and references therein (see Table 1 for voucher information and GenBank accession numbers). The datasets were subjected to maximum likelihood (ML) analysis in RAxML v. 8.2.0 (Stamatakis 2014) under the GTR-Gamma model. Branch support was assessed by bootstrapping (100 replicates). Phylogenetic trees were visualized and edited in FigTree v. 1.4.4 (Rambaut 2018) and Inkscape v. 0.92 graphic software (http://inkscape.org).

The current phylogenetic analyses are a continuation of the study started by Wilk & al. (2021), and the phylogenetic *Teloschistaceae* tree therein was used as reference tree for this survey.

Table 1. Sequences downloaded from GenBank and used in the phylogenetic analyses.

Species	Reference	Voucher	ITS	nucLSU	mtSSU
Blastenia ammiospila	Arup & al. 2013	Austria, Søchting 9345, C (ITS, mtSSU); Norway, Søchting 10092, C (nucLSU)	KC179413	KC179161	KC179491
Blastenia crenularia	Arup & al. 2013	Iceland, Søchting 7523, C	KC179415	KC179162	KC179492
Bryoplaca sinapisperma	Arup & al. 2013	Norway, Arup L08184, LD	KC179421	–	KC179495
Bryoplaca tetraspora	Arup & al. 2013	Antarctica, South Shetland Isl. Søchting 7979, C (ITS); Denmark, Greenland, Søchting 10480, C (mtSSU)	KC179422	–	KC179496
Calogaya alaskensis	Arup & al. 2013	Sweden, Arup L04335, LD	KC179341	–	–
Calogaya arnoldii 1	Arup & al. 2013	Sweden, Arup L06205, LD (ITS); Sweden, Søchting 10610, C (nucLSU)	KC179342	KC179165*	–
Calogaya arnoldii 2	Gaya & al. 2008	France, Clauzade s.n., MARSSJ holotype	EU639633	–	–
Calogaya arnoldii s.l.	Arup & al. 2013	Denmark, Søchting 7472, C	KC179343	KC179166*	KC179497*
Calogaya arnoldii subsp. *obliterata*	Gaya & al. 2012	Sweden, Gaya & al. s.n., BCN	JQ301657	JQ301547*	JQ301481*
Calogaya arnoldiiconfusa	Arup & al. 2013	Austria, Hafellner s.n., GZU	HM800875	–	–
Calogaya biatorina 1	Arup & al. 2013	Austria, Arup L97807, LD	AF353953	–	–
Calogaya biatorina 2	Gaya & al. 2011	Spain, Søchting 9608, BCN	HM800895	–	–
Calogaya biatorina 3	Gaya & al. 2011	Spain, Gaya 267 & al., BCN	HM800897	–	–
Calogaya biatorina 4	Gaya & al. 2011	USA, Montana, Wetmore 81529, MIN	HM800898	–	–
Calogaya decipiens	Arup & al. 2013	Denmark, Søchting s.n., C	KC179344	KC179167*	KC179498*
Calogaya lobulata 1	Arup & al. 2013	Poland, Cieśliński s.n., GZU	KC179345	–	–
Calogaya lobulata 2	Kondratyuk & al. 2014b	Australia, Tasmania, Kärnefelt 9977001, KW-L	KJ133449	KJ133488*	KJ133507*
Calogaya miniata 1	Gaya & al. 2011	Spain, Gaya 273 & al., BCN	HM800883	–	–
Calogaya miniata 2	Gaya & al. 2011	Spain, Navarro-Rosinés 390, BCN	HM800884	–	–
Calogaya miniata 3	Gaya & al. 2011	Austria, Poelt & al. s.n., GZU	HM800885	–	–
Calogaya polycarpoides	Arup & al. 2013	Kazakhstan, Seaward s.n., Seaward priv. herb.	KC179346	–	–
Calogaya pusilla 1	Arup & al. 2013	Sweden, Arup L07089, LD	KC179347	–	–
Calogaya pusilla 2	Gaya & al. 2011	Slovakia, Pisút & Poelt s.n., GZU	HM800890	–	–
Calogaya saxicola 1	Gaya & al. 2011	Canada, Northwest Territories, Gould 945, MIN	HM800882	–	–
Calogaya saxicola 2	Gaya & al. 2011	USA, Wyoming, Wetmore 80927, MIN	HM800887	–	–
Calogaya saxicola 3	Gaya & al. 2011	USA, Nebraska, Wetmore 77946, MIN	HM800870	–	–
Calogaya schistidii	Arup & al. 2013	Austria, Arup L97464, LD	KC179348	–	–

Species	Reference	Voucher	ITS	nucLSU	mtSSU
Calogaya sp.	Arup & al. 2013	Argentina, Frödén 1728, LD	KC179349	–	–
Caloplaca cerina	Arup & al. 2013	Norway, Svalbard, Elvebakk 03:084, TROM	KC179425	KC179168	KC179499
Caloplaca chlorina	Arup & al. 2013	Sweden, Frödén 1876, LD (ITS); Denmark, Søchting 7321, C (nucLSU, mtSSU)	KC179426	KC179169	KC179500
Caloplaca turkuensis	Arup & al. 2013	Sweden, Frödén 1909, LD	KC179432	–	KC179501
'Caloplaca' aggregata	Kondratyuk & al. 2017	Australia, Kantvilas 476/12, HO holotype	KY614390	KY614448	KY614479
'Caloplaca' albolutescens	Arup & al. 2013	Sweden, Arup L09030, LD	KC179423	–	KC179502
'Caloplaca' atroflava	Arup & al. 2013	Sweden, Arup L06010, LD	KC179424	KC179171	KC179504
'Caloplaca' demissa	Arup & al. 2013	Italy, Arup L97911, LD	AF353960	KC179172	KC179505
'Caloplaca' fernandeziana	Vargas Castillo & Beck 2012	Chile, Vargas 2415 & Stanton, M	JQ993841	–	–
'Caloplaca' furax	Gaya & al. 2012	Spain, Gaya, Fernández-Brime 557 & Llimona, BCN	JQ301662	JQ301554	JQ301490
'Caloplaca' lecanorocarpa	Aptroot & Cáceres 2016	Brazil, Aptroot & Cáceres 21364, ISE holotype	KU257734	–	–
'Caloplaca' lecapustulata	Aptroot & Cáceres 2016	Brazil, Aptroot & Cáceres 21383, ISE holotype	KU257735	–	–
'Caloplaca santessoniana' ad int. (sub. *Caloplaca* sp. EG-2015a in GB)	Gaya & al. 2015	Chile, Gaya 19.2.11- 37 & Vargas, DUKE	KT291463	KT291558	KT291508
Catenarina desolata	Søchting & al. 2014a	Chile, Søchting 10436a, C	KF657317	–	KF657319
Catenarina vivasiana	Søchting & al. 2014a	Chile, Søchting 10410, C	KF657312	–	KF657318
Eilifdahlia dahlii	Kondratyuk & al. 2014a	Australia, Kärnefelt 20043101, LD	KJ021318	KJ021253	KJ021279
Eilifdahlia wirthii	Kondratyuk & al. 2014a	Namibia, Wirth & al. s.n., KW holotype	KJ021319	KJ021254	KJ021280
Franwilsia bastowii	Kondratyuk & al. 2014a	Australia, Kärnefelt 994301, LD	KJ021324	KJ021257	KJ021284
Franwilsia kilcundaensis	Kondratyuk & al. 2014a	Australia, Kondratyuk 20423, LD	KJ021326	KJ021259	KJ021286
Gyalolechia aurea	Arup & al. 2013	Austria, Arup L97493, LD (ITS, mtSSU); Austria, Poelt & Grube s.n., GZU (nucLSU)	KC179434	KC179196	KC179530
Gyalolechia flavorubescens	Arup & al. 2013	Estonia, Søchting 10127, C	KC179439	KC179197	KC179531
Gyalolechia gomerana	Arup & al. 2013	Spain, Søchting 9653, C	KC179441	KC179200	KC179534
Huneckia crocina	Wilk & al. 2021	Bolivia, Wilk 2507, KRAM	MT754239	MT835245	MT754207
Huneckia pollinii 1	Kondratyuk & al. 2014a (incorrect GenBank numbers cited)	USA, Missouri, Wetmore 84103, LD1061948	KJ021337	KJ021266	KJ021297
Huneckia pollinii 2	Kondratyuk & al. 2014a (incorrect GenBank numbers cited)	USA, Kansas, Morse 14464, LD 1276205	KJ021338	KJ021267	KJ021298
Huneckia rheinigera	Kondratyuk & al. 2014a	Australia, Queensland, Elix 28833, LD isotype	KJ021222	–	–

Species	Reference	Voucher	ITS	nucLSU	mtSSU
÷*Leproplaca chrysodeta*	Arup & al. 2013	Sweden, Arup L7107, LD	KC179448	KC179206	–
Leproplaca obliterans	Arup & al. 2013	Sweden, Arup L02331, LD (ITS, mtSSU); Norway, Arup L03472, LD (nucLSU)	KC179449	KC179207	KC179541
Pyrenodesmia chalybaea	Arup & al. 2013	Austria, Søchting 9351, C (ITS, mtSSU); Sweden, Gotland, Gaya s.n. & al., BCN (nucLSU)	KC179454	JQ301550	KC179571
Pyrenodesmia variabilis	Arup & al. 2013	Austria, Arup s.n., LD (ITS); Sweden, Arup L03134, LD (nucLSU, mtSSU)	AF353963	KC179234	KC179572
Rufoplaca scotoplaca	Arup & al. 2013	Sweden, Arup L10032, LD	KC179457	KC179235	KC179573
Rufoplaca tristiuscula	Arup & al. 2013	Norway, Arup L08171, LD	KC179460	KC179237	KC179575
Seirophora lacunosa	Arup & al. 2013	Kazakhstan, Moberg & Nordin K18:04, LD	KC179465	KC179243	KC179582
Seirophora scorigena	Arup & al. 2013	Spain, Lanzarote & Snogerup 17201, LD	KC179466	KC179244	KC179583
Squamulea subsoluta	Arup & al. 2013	Austria, Arup L97072, LD	AF353954	KC179253	KC179592
Usnochroma carphineum	Arup & al. 2013	France, Roux s.n., C	KC179468	KC179259	KC179598
Variospora aurantia	Arup & al. 2013	Spain, Llimona s.n., C (ITS, mtSSU); Italy, Lange s.n., C (nucLSU)	KC179470	KC179261	KC179600
Variospora dolomiticola	Arup & al. 2013	Spain, Thell SP0514, LD	KC179471	KC179262	KC179601
Variospora velana	Arup & al. 2013	Italy, Arup L07194, LD (ITS); Italy, Arup L07123, LD (nucLSU, mtSSU)	KC179476	KC179265	KC179605
Wetmoreana brouardii	Gaya & al. 2015	Mexico, Baja California, Gaya 03.03.10-3 & Lutzoni, DUKE	KT291448	KT291536	–
Wetmoreana decipioides 1	Arup & al. 2013	South Korea, Thor 20768, UPS holotype	KC179333	KC179269	KC179608
Wetmoreana decipioides 2	Kondratyuk & al. 2013	South Korea, Joshi & al. 100317, KoLRI	KF264643	–	KF264694
Wetmoreana decipioides 3	Kondratyuk & al. 2013	South Korea, Joshi & al. 100327, KoLRI	KF264644	–	KF264695
Wetmoreana decipioides 4	Gaya & al. 2015	South Korea, Thor 20768, UPS holotype	KT291453	KT291540	KT291487
Wetmoreana sp. 1	Arup & al. 2013	Chile, Frödén 1645, LD	KC179334	KC179270	KC179609
Wetmoreana sp. 2	Arup & al. 2013	Peru, Frödén 1519, LD	KC179335	KC179271	KC179610
Wetmoreana sp. 3	Arup & al. 2013	Peru, Frödén 1521, LD	KC179336	KC179272	KC179611
Wetmoreana texana 1	Arup & al. 2013	Mexico, Søchting 9925, C	KC179337	KC179273	KC179612
Wetmoreana texana 2	Gaya & al. 2008	Mexico, Wetmore 79365, BCN	EU639656	–	–
Xanthoria parietina	Arup & al. 2013	Denmark, Søchting s.n., C	KC179411	KC179289*	KC179629*

* sequences available in GenBank but not used in this study

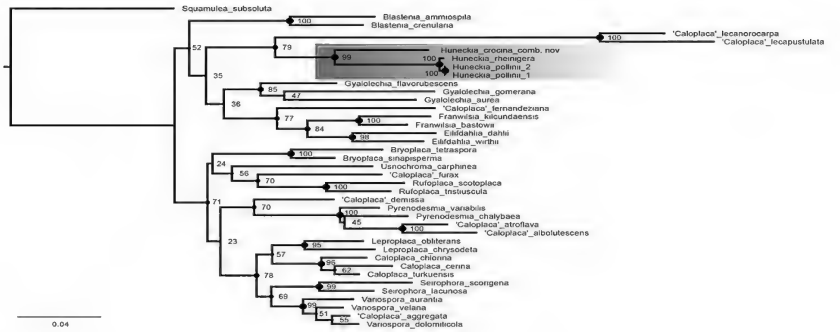

Fig. 1. Phylogenetic placement of *Huneckia crocina* within the subfamily *Caloplacoideae* derived from maximum likelihood (ML) analyses of rDNA ITS, nucLSU, and mtSSU loci. ML bootstrap values are presented at the nodes. *Squamulea subsoluta* was used to root the tree. *Huneckia* genus, including *H. crocina*, is marked with grey.

Phylogenetic results

The phylogenetic analyses based on three rDNA loci (ITS, nuLSU and mtSSU) nest *Caloplaca crocina* within *Caloplacoideae* with a strongly supported (BS = 99) sister relationship to *Huneckia pollinii* and *H. rheinigera* (Fig. 1; see also Wilk & al. 2021: Fig. 1, Suppl. Fig. 1). Within the *C. crocina* clade is clearly separated from the latter two species by its long branch. The *Huneckia* clade is sister to *'Caloplaca' lecapustulata* Aptroot & M. Cáceres and *'C.' lecanorocarpa* Aptroot & M. Cáceres, but with only moderate support (BS = 79). The relationship of *Huneckia* to other representatives of *Caloplacoideae* is resolved without support, indicating its close relationship to *Blastenia* A. Massal., *Eilifdahlia* S.Y. Kondr. & al., *Franwilsia* S.Y. Kondr. & al., *Gyalolechia* A. Massal., and *'Caloplaca' fernandeziana* (Zahlbr.) Follmann & Redón. Before our research, the phylogenetic position of *C. crocina* was unknown, although its potential placement in *Huneckia* could be inferred based on certain morphological characters, especially the thick walls of the ascospores. Thick-walled ascospores, however, cannot be treated as distinctive for the genus, because this type of ascospore occurs also in *Flavoplaca* Arup & al. [e.g., *F. dichroa* (Arup) Arup & al. and *F. calcitrapa* (Nav.-Ros. & al.) Arup & al.; *Xanthorioideae*].

The phylogenetic analyses based on three-loci dataset (ITS, nuLSU, and mtSSU) nests *Caloplaca rouxii* within *Calogaya* (*Xanthorioideae*) (Wilk & al. 2021: Fig. 1, Suppl. Fig. 1). Within the *Calogaya* clade *C. rouxii*, *C. arnoldiiconfusa* Gaya & Nav.-Ros., and *C. saxicola* (Hoffm.) Nordin form a

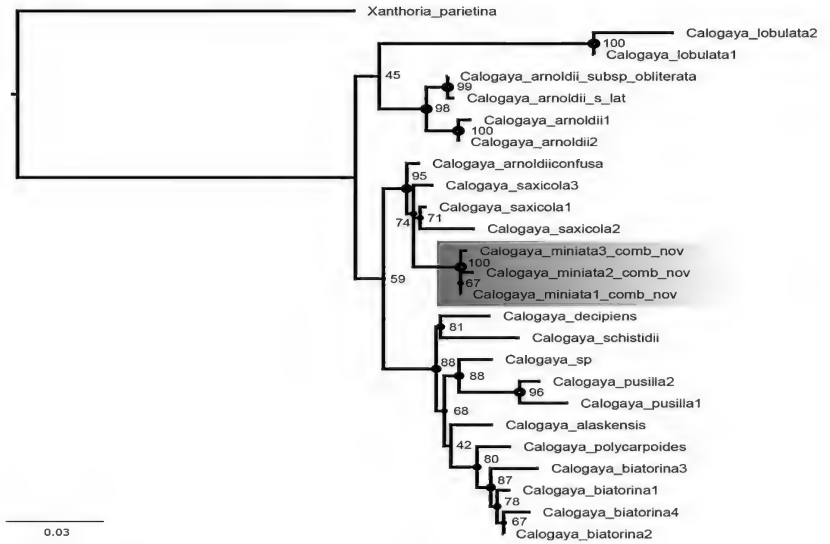

FIG. 2. Phylogenetic placement of *Calogaya miniata* (marked in grey) within the subfamily *Xanthorioideae* derived from maximum likelihood (ML) analyses of rDNA ITS locus. ML bootstrap values are presented at the nodes. *Xanthoria parietina* was used to root the tree.

well-supported (BS = 95) group of closely related taxa (FIG. 2). The phylogenetic position of *Caloplaca rouxii* within *Calogaya* was also studied in detail by Gaya & al. (2011), who noted the monophyly of *C. rouxii*, while *C. saxicola* appears monophyletic or polyphyletic depending on the phylogenetic analysis. The polyphyly of *C. saxicola* has been discussed in detail by Gaya & al. (2011) and Vondrák & al. (2018).

Taxonomy: new combinations

Calogaya miniata (Hoffm.) Wilk & Lücking, **comb. nov.**

MB 839870

≡ *Psora miniata* Hoffm., Enum. Lich.: 63 (1784); Descr. Pl. Cl. Crypt. 3(2): 16 (1801).

TYPE: Spain. Catalunya, Lleida, Alt Urgell, Fígols I Alinyà, entre el Perdó dels Quatre Batlles I el Prat Llarg, elev. 2200–2382 m, 2001, Navarro-Rosinés (BCN, neotype, designated by Gaya 2009).

≡ *Lichen miniatus* Hoffm., Enum. Lich.: 62 (1784) [nom. illeg., ICN (Shenzen) Art. 53, non *Lichen miniatus* L 1753].

≡ *Lobaria miniata* (Hoffm.) Hoffm., Deutschl. Fl. 2: 158 (1796) ["1795"].

≡ *Caloplaca rouxii* Gaya, Nav.-Ros. & Llimona, Biblioth. Lichenol. 101: 82 (2009) [nom. illeg., ICN (Shenzen) Art. 52].

For taxonomic description, distribution, illustrations, and further synonyms, see Gaya (2009).

Nomenclatural notes—*Calogaya miniata* was first described by Hoffmann (1784: 62), under the name *Lichen miniatus* Hoffm., an illegitimate later homonym of *L. miniatus* L. Gaya (2009) proposed *Caloplaca rouxii* as a replacement name for the illegitimate *L. miniatus* Hoffm. However, Hoffmann (1784: 62–63) had originally published two alternative names (*L. miniatus* and *Psora miniata*) for this species, both of which are valid [ICN (Shenzhen) Art. 36.3], but as *Lichen miniatus* Hoffm. is illegitimate, *Psora miniata* remains the legitimate basionym of the species, a name also used in a subsequent treatment of the species by the same author (Hoffmann 1801). Gaya's (2009) replacement name *Caloplaca rouxii* is superfluous and illegitimate, because Gaya (2009) cited *Lichen miniatus* Hoffm. as the replaced synonym and *Psora miniata* is an alternative name based on the same type [ICN (Shenzhen) Arts 52.1, 52.2(e)].

Hoffmann (1796: 158) also published the combination *Lobaria miniata*, based on *Lichen miniatus* Hoffm. Subsequently, this has been interpreted as being based on *Lichen miniatus* L., being cited as *Lobaria miniata* (L.) Hoffm. and interpreted as a homotypic synonym of *Dermatocarpon miniatum* (L.) W. Mann. However, Hoffmann's combination is clearly based on *Lichen miniatus* Hoffm., not *L. miniatus* L., both explicitly ["Enum. Lich. *62.* (*Lich. miniatus*)"] and implicitly by describing the lichen as "foliois ... miniatis," i.e., scarlet or cinnabar-red, and not grey as in *D. miniatum*. The correct citation of this combination is therefore *Lobaria miniata* (Hoffm.) Hoffm. If Hoffmann had not already established the alternative name *Psora miniata* twelve years prior in 1784, *Lobaria miniata* (as a replacement name for *L. miniatus* Hoffm.) would have had priority over the erroneously presumed first publication of *Psora miniata* five years later in 1801.

Hoffmann (1784) did not cite any material in the protologue of *Lichen miniatus*/*Psora miniata*. Later he provided a color plate under the name *Psora miniata* (Hoffmann 1801: Tab. LX). However, as it cannot be established that this illustration and its underlying specimen were part of the original material, they are not available for lectotypification and have no priority in terms of typification. The neotypification proposed by Gaya (2009) is therefore appropriate.

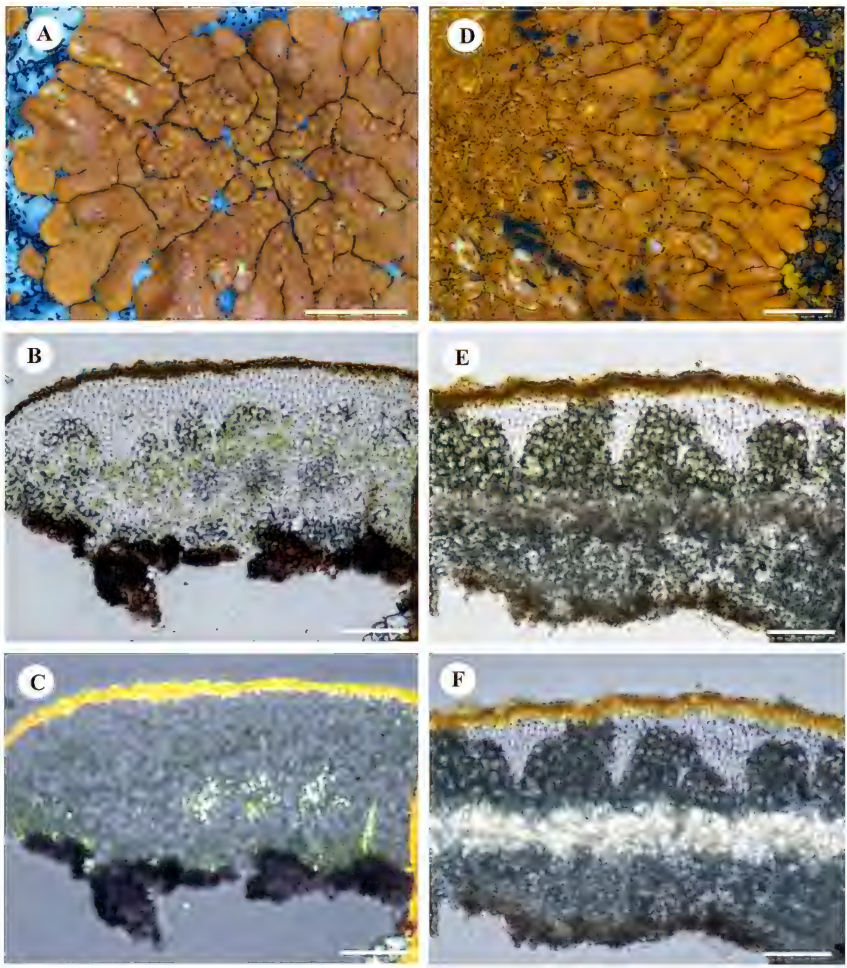

Fig. 3. ***Wetmoreana brouardii***, habitus and cross section of thallus: A. Wetmore 69973 (MIN); B, C. Wetmore 79665 (MIN). ***Caloplaca ochraceofulva***, habitus and cross section of thallus: D. Geesteranus 10299 (LD); E, F. Kofler (LD1066528). B, E = in regular light; C, F = in polarized light. Scale bars: A = 2.5 mm; B, C, E, F = 50 μm; D = 2 mm.

Huneckia crocina (Kremp.) Wilk, **comb. nov.**

MB 836903

≡ *Lecidea crocina* Kremp., Flora 61: 519 (1878).

Type: Argentina. 1873–1874, Lorentz & Hieronymus (M!, holotype).

≡ *Caloplaca crocina* (Kremp.) Wilk & R. Vargas, Mycotaxon 132: 127 (2017).

Additional synonyms, taxonomic description, distribution, and illustrations are available in Wilk & Flakus (2017).

Taxonomic notes—*Huneckia* includes three species: *H. pollinii* (type species), *H. rheinigera* (Kondratyuk & al. 2014a), and the newly transferred *H. crocina*. These species are morphologically similar to one another. They produce continuous to areolate grayish thalli and dark orange to brownish, biatorine or zeorine apothecia. The apothecial margin (true exciple) is prosoplectenchymatous, composed of radiating, conglutinating hyphae. The ascospores are polarilocular, characterized by clearly thickened terminal spore walls (also called hourglass-shaped, sand-clock, or sand-glass types). The diagnostic characters for these and similar *Caloplaca* s.lat. species are discussed in Wilk & Flakus (2017: Table 1). *Huneckia* is characterized by specific anthraquinones, mainly chrysophanol, chrysophanal and rhein (Kondratyuk & al. 2014a), although the chemical composition of lichen secondary metabolites present in *H. crocina* has not been studied. The genus is mostly similar to *Blastenia*. For characters distinguishing among these taxa see Vondrák & al. (2019). *Huneckia pollinii* is widespread in the Northern Hemisphere (Wetmore 1994; Miao & al. 2018), *H. rheinigera* is known from Australia (Kondratyuk & al. 2007), and *H. crocina* is common in South America (Wilk & Flakus 2017). *Huneckia pollinii* and *H. rheinigera* are well-illustrated in Schumm & Aptroot (2019a,b) and *H. crocina* in Wilk & Flakus (2017).

Taxonomy: new records

Wetmoreana brouardii (B. de Lesd.) Wilk & Søchting,
Pl. Fung. Syst. 65(2): 562. 2020. Fig. a–c

A taxonomic description is available in Wetmore & Kärnefelt (1998).

Specimens examined—**CHILE. Valparaíso**, Cuesta de Chacabuco, Follmann 12885 (B). **COLOMBIA. Cundinamarca, Nariño**, Munic. Imues, near El Pedregal, towards Túquerres, on road Pasto-Tumaco, elev. 1880 m, 16 June 1986, Sipman 33540 (B). **PERU. Dept. Arequipa, Prov. Caylloma**, Cañon del Colca canyon, below Tapay village, open semi-desert montane area, elev. 2774 m, 6 July 2006, Flakus 9663 & Cykowska (KRAM; fertile specimen). **URUGUAY. Dept. Canelones**, Parador Tajes, El Cerroto, elev. 10–20 m, 19 Feb 1950, Osorio 2135 (B). **MEXICO. Baja California Sur, Sierra Laguna**, along river bottom Picacho de La Laguna, elev. 500 m, 16 Feb 1993, Wetmore 72011 (B), open oak forest (*Quercus tuberculata*) with shrubs, along ridge leading to the crest after turnoff to Rancho La Victoria, elev. 1400 m, 6 Jan 1998, Wetmore 79665 (MIN). **Chihuahua, Sierra la Cinguita**, eastern side, 9 km west of Moctezuma along route 10, elev. 1120 m, 16 March 1992, Wetmore 69973 (MIN).

material investigated for comparison—***Caloplaca ochraceofulva***. (Fig. 3, d–f) **KENYA. Rift Valley Province**, distr. Nakuru, 1949, Geesteranus 10299 & L4644a

Table 2. Comparison of *Wetmoreana brouardii* and *Caloplaca ochraceofulva*

Characters	*W. brouardii*	*C. ochraceofulva*
Vegetative propagules	Papillae, laminal	Isidia, marginal
Spores (µm)	10–13 × 4–6	10–16 × 4–8
septum (µm)	2.5–3.5	2–4
Thallus	Thin	Thick
lobe thickness (µm)	90–250	130–400
Cortex	Cell lumina rounded	Cell lumina elongated
Cortex cones	Absent or indistinct	Distinct
Algae	Continuous	Discontinuous, in distinct groups
Medulla	Thin, indistinctly separated from the algae layer	Thick, distinctly separated
CaOx crystals	Absent (medulla may illuminated in polarized light due to the lichen substances, in K & N insoluble)	Distinct layer (35–75 µm thick; in K insoluble, in N soluble) at a distance of c. 100 µm from the thallus surface, on the border between algal layer and medulla
Pycnidia	Rare	Common
Conidia (µm)	Long bacilliform, 4.0 × 1.1 (mean)	Short bacilliform or ovoid, 3.1 × 1.2 (mean)
Substrate	Siliceous rocks	Siliceous or calcareous rocks
Distribution	Widespread in Americas, and Arabian Peninsula	Widespread in Africa, and Arabian Peninsula and South America
References	This paper	This paper

(LD). **LESOTHO. Leribe**, Buthabuthe, 1963, Kofler s.n. (LD1066528, LD1066592), Kopje near Buthabuthe, 1963, Kofler s.n. (LD1024127). **NAMIBIA, Otjozondjupa Region**, Waterberg Plateau National Park, primary forest with large *Ficus* at the base of Waterberg Plateau, elev. 1469 m, 15 June 2019, Flakus 19/162 (KRAM, DUKE). **SOMALILAND. Serrubgebirge**, 1885, Hildebrandt s.n. (G66459, Lectotypus). **SOUTH AFRICA. Natal**, Vryheid Div., 1953, Almborn 7976 (LD1024960, LD1024896; fertile specimens). **Orange Free State**, Div. Ladybrand, 1949, Geesteranus L6546 (LD). **SAUDI ARABIA. Asir Region, Al Dalaghan area**, Asir National Park, 1982, Zapletal s.n. (BM1247493, E905776, E905777). **ARGENTINA, Jujuy**, Santa Barbara, 1901, Fries 50 (LD). **URUGUAY, Dept. Maldonado**, Rio de la Plata, Isla Gorriti, 1984, Osorio 8345 (MIN).

Taxonomic note—*Wetmoreana brouardii* is characterized by the clearly lobate, thin thallus, closely appressed to the substratum. The thallus is orange to reddish, abundantly covered by distinct, laminal papillae. According to Wetmore & Kärnefelt (1998) apothecia are very rare, sessile, and ≤0.5 mm; the ascospores are polarilocular (11–14 × 5.5–7.0 µm) with a 3.5–4.0 µm thick septum.

Wetmoreana brouardii is often misidentified as *Caloplaca ochraceofulva*, which is closely related (Wilk & Lücking, unpubl. data) but which differs from

W. brouardii in having a distinctly thicker, yellow-orange (not reddish) and isidiate thallus. Another distinguishing feature is the presence or absence of calcium oxalate crystals (pol+ white) in the thallus. They are present in *C. ochraceofulva*, forming a distinct layer along the border between the algal layer and medulla, but absent in all studied material of *W. brouardii* (Fig. 3, Table 2). Medullary crystals are diagnostic for other *Wetmoreana* species, such as *W. appressa, W. texana*, and the probably related *Caloplaca eugyra* (Tuck.) Zahlbr. (Wetmore & Kärnefelt 1998).

Habitat and distribution—*Wetmoreana brouardii* occurs on siliceous rocks. It was reported from North America in Mexico and USA (Nash & al. 1998; Wetmore & Kärnefelt 1998); from the Arabian Peninsula in Saudi Arabia (Bokhary & al. 1993) and Qatar (Al-Thani & Al-Meri 2011); from Central America in Guatemala (Wetmore & Kärnefelt 1998), and from South America in Brazil (Aptroot & al. 2017), Ecuador (Galapagos Islands), (Bungartz & al. 2013), and Venezuela (Aptroot 2015).

New records of *Wetmoreana brouardii* are reported here from Chile, Peru, Uruguay, and Colombia. The Peruvian material cited previously by Wetmore & Kärnefelt (1998) lacked locality data, provided here.

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Kirschsteiniothelia shimlaensis sp. nov. from Himachal Pradesh, India

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Abstract—A new species, *Kirschsteiniothelia shimlaensis* collected on stumps of *Cedrus deodara*, is described and illustrated. It is characterized by mostly monotretic (rarely polytretic), terminal or intercalary, discrete or integrated conidiogenous cells with solitary conidia that are obovoid, oblong, broadly clavate or cylindrical and dark brown, smooth, and 2–5-septate.

Key words—anamorphic fungi, hyphomycetes, *Kirschsteiniotheliaceae*, taxonomy

Introduction

Himachal Pradesh is situated at 30°22′40″–33°12′40″N 75°45′55″–79°04′20″E. Elevations in the state, a wholly mountainous region in the lap of Himalayas, range from 350 to 6975 m. Himachal Pradesh can be divided

into three distinct regions, the [1] Shivalik or outer Himalayas, [2] middle or inner Himalayas, and [3] greater Himalayas or alpine zone. Of the total area (55,673 km^2), 25.8% is under forest cover and offers a vast variety of perennial plants (Balokhra 2011). Since the Himachal Pradesh with different climatic regions supports both tropical and temperate vegetation, the extensive growth of fungi is predictable. Terrestrial saprobic hyphomycetes are an important component of Himalayan forest ecosystem as they play an important role in nutrient cycling. Studies on the fungal diversity of the Northwestern Himalayan ecosystem with particular reference to Himachal Pradesh have been primarily restricted to *Agaricomycetes* (Prasher & Ashok 2013, Ashok & Prasher 2014a,b). There are only few reports of hyphomycetes from this area (Bilgrami & al. 1991, Jamaluddin & al. 2004, Prasher & Verma 2012a,b, 2014a,b, 2015a,b,c). The hyphomycete records reported from this region pertain primarily to plant pathogenic fungi affecting crops (Bilgrami & al. 1991, Jamaluddin & al. 2004). Other new records of hyphomycetous fungi from India have been added by Prasher & Sushma (2014), Verma & al. (2019), and Sushma & al. (2020).

Kirschsteiniothelia D. Hawksw., typified by *K. aethiops* (Sacc.) D. Hawksw., is distinguished by ostiolate ascomata with pseudoparenchymatous peridium of textura angularis to prismatica and composed of subglobose or polyhedral cells. The centrum comprises cellular, branched pseudoparaphyses and bitunicate, fissitunicate, subcylindrical or elongate-clavate asci with (4–)8 ellipsoidal or soleiform, 1-septate, distichously arranged ascospores that are slightly constricted at the septum, brown, verruculose or striate, and covered by a distinct gelatinous tunica. Conidiophores are macronematous; mononematous; erect, straight or flexuous; and branched toward the apex, with the branches irregular or scorpioid. Conidiogenous cells are monotretic, cylindrical or doliiform, mostly discrete (sometimes integrate), determinate or with enteroblastic percurrent elongations, brown. The solitary conidia are cylindrical, obclavate, clavate, oblong, or obovoid; straight or slightly curved; 2 or more septate; and olivaceous-brown, brown, or black (Boonmee & al. 2012 Hawksworth. 1985, Su & al. 2016).

Wijayawardene & al. (2014) demonstrated that *Dendryphiopsis atra* (Corda) S. Hughes (the type of *Dendryphiopsis* S. Hughes) belonged in *Kirschsteiniothelia;* however, further phylogenetic analyses are required to ascertain the correct generic affinities with other *Dendryphiopsis* species. During a mycological survey of microfungi associated with culm, twigs and decaying wood in a Himachal Pradesh forest, a conspicuous fungus was collected, which we propose here as a new *Kirschsteiniothelia* species.

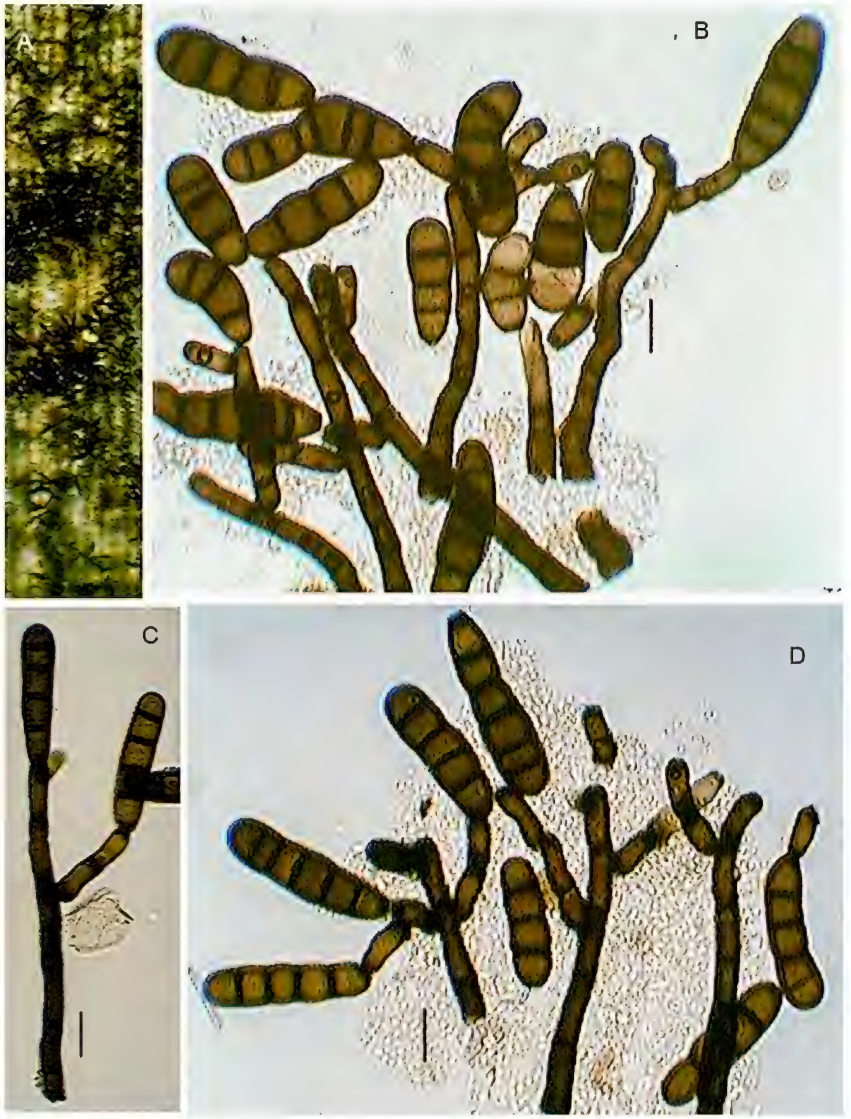

Fig. 1. *Kirschsteiniothelia shimlaensis* (holotype, PAN 30505). A. Colonies on natural substratum. B–D. Conidiophores, conidiogenous cells with attached conidia. Scale bars: B–D = 20 µm.

Materials & methods

Decaying culms, twigs and wood were collected in zip lock bags and taken to the laboratory. The specimens were mounted in 4% KOH, lactophenol, and 0.01% cotton blue in lactophenol (Kirk & al. 2008). The specimens were studied microscopically under Matrix VL–Z60 stereo trinocular microscope and VRS–2f compound microscope. All measurements were taken with ProMED software. The specimen was deposited in the herbarium of Botany Department, Panjab University, Chandigarh, India (PAN).

Taxonomy

Kirschsteiniothelia shimlaensis Rajn.K. Verma, Prasher, Rajeshk., Sushma, A.K. Gautam & R.F. Castañeda, **sp. nov.** FIGS 1, 2

IF 557827

Differs from *Kirschsteiniothelia atra* by its obovoid, oblong, broadly clavate, narrower conidia.

TYPE: India. Himachal Pradesh: Shimla, Kumarsain, on decaying stump of *Cedrus deodara* (Roxb. ex D. Don) G. Don, 19 Nov. 2016, R.K. Verma (**Holotype**, PAN 30505).

ETYMOLOGY: Latin, *shimlaensis,* referring to the place of collection, Shimla district.

COLONIES on natural substratum scattered, dark, brown to black. Mycelium partly superficial, partly immersed in the host tissue. CONIDIOPHORES macronematous, mononematous, single to loosely fasciculate, erect, straight to flexuous multiseptate, irregular or subscorpioid branched at the apex, dark brown, smooth, 110–268 × 12–19 µm, 7–9 µm wide at the apex. CONIDIOGENOUS CELLS monotretic, terminal or intercalary, cylindrical or doliiform, mostly discrete, determinate, sometimes with enteroblastic percurrent elongations, smooth, dark brown or brown, 18–24 × 8–10 µm. CONIDIA solitary, obovoid, oblong, broad clavate or cylindrical, sometimes constricted near the middle or at the supra basal cell, sub-truncate or rounded at the base, rounded at the apex, dark brown or black, smooth, microguttulate, lumen aspect granulose, 2–5(–6)-septate, 41–81 × 13–17.5 µm.

Discussion

Kirschsteiniothelia shimlaensis is superficially similar to *K. atra* (Corda) D. Hawksw., which differs in its mostly cylindrical, pale to mid-dark smoky or olivaceous brown, and wider (12–25 µm) conidia (Ellis 1971, Hughes 1953, 1958; as "*D. atra*"). *Kirschsteiniothelia shimlaensis* also differs from *K. lignicola* Boonmee & K.D. Hyde which has ellipsoidal to obovate, 2-septate conidia, and *K. emarceis* Boonmee & K.D. Hyde which has oblong to obclavate, 3–4-septate conidia (Boonmee & al. 2012.

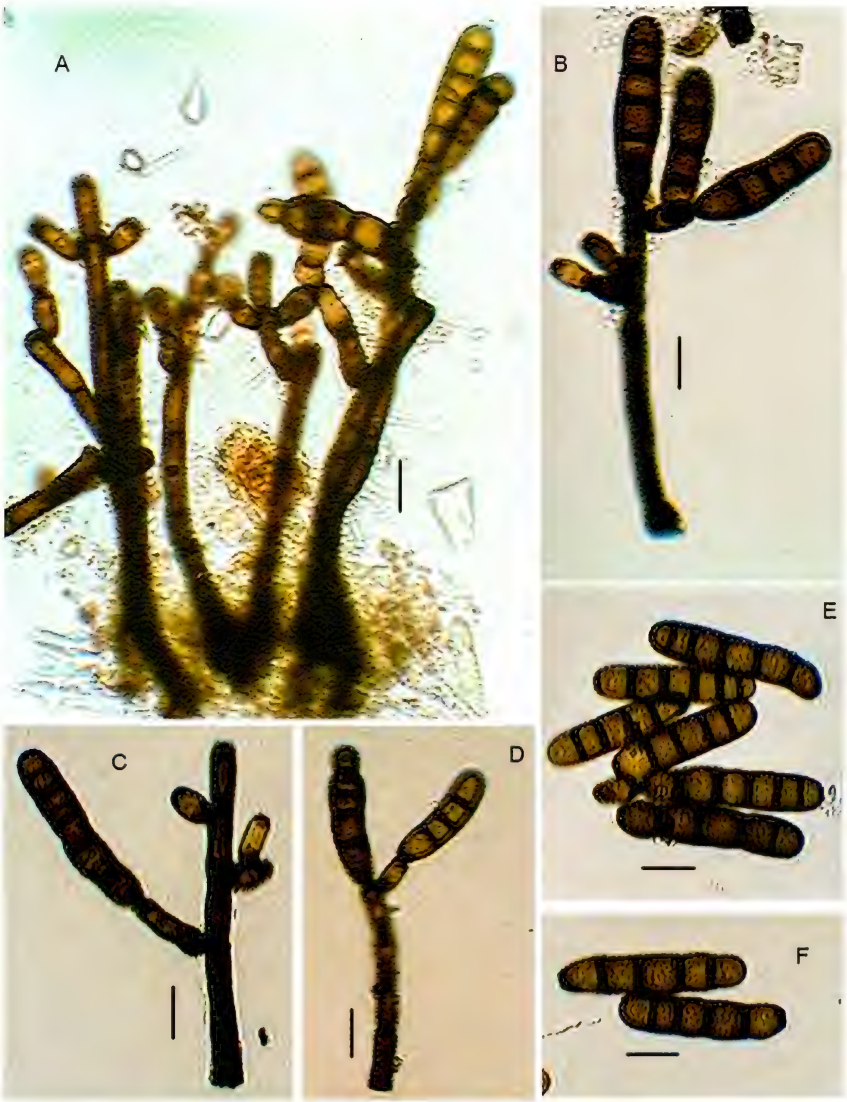

Fig. 2. *Kirschsteiniothelia shimlaensis* (holotype, PAN 30505). A–D. Conidiophores, conidiogenous cells with attached conidia. E,F. Conidia. Scale bars = 20 μm.

Dendryphiopsis goaensis J. Pratibha & al., shares a somewhat similar conidial morphology with *K. shimlaensis,* but *D. goaensis* has mostly cylindrical, dark brown, 20–40 × 5–7.5 µm conidia, frequently produced in polytretic conidiogenous cells (Pratibha & al. 2010). Other *Dendryphiopsis* species comparable with *K. shimlaensis* are *D. arbuscula* (Berk. & M.A. Curtis) S. Hughes, *D. binsarensis* Subram. & V. Srivast., and *D. fascicularis* (Berk. & Ravenel) S. Hughes; *D. arbuscula* is distinguished by conidia that are subfusiform, fusiform or obclavate 3-7-septate, blackish olivaceous, 50–80 × 14–17 µm (Berkeley 1875, Ellis 1976), *D. binsarensis* has obclavate to obclavate-fusiform, 3-7-septate, brown conidia, 36–44 × 8–10 µm (Subramanian & Srivastva 1994), and *K. fascicularis* has long-clavate conidia, strongly attenuated at the base (Berkeley 1875, Hughes 1958).

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A key to the identification of the genera of lichenized fungi occurring in Thailand

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Abstract—A key to the identification of the 258 genera of lichenized fungi in Thailand is presented. Species names are provided for genera for which only a single species has been recorded for Thailand. Recent available keys that include all species known from Thailand are referenced. The replacement name *Ionaspis aptrootii* is proposed for *I. tropica* Aptroot (non Riddle).

Key words—biodiversity, lichens, Southeast Asia, tropics

Introduction

The lichen flora of Thailand has recently received considerable interest resulting in more than a doubling of the known species in only 15 years between a first catalogue (Wolseley & al. 2002) and a recent checklist (Buaruang & al. 2017). Moreover, several treatments of genera or species groups of lichenized fungi in East Asia or focused on Thai species have been published (cited below in the key) improving our knowledge of species diversity. Recently, numerous phylogenetic studies have dramatically changed our understanding of the evolution of lichenized fungi, with numerous taxonomic changes at the generic rank which are summarized elsewhere (Jaklitsch & al. 2016, Lücking & al. 2016a, 2017). However, only few keys to the

genera of tropical lichens, especially crustose taxa, are available, providing an impediment to the training of students and making species-based treatments for scientists less accessible. For these reasons, we are providing a key to the identification of lichen genera in Thailand and notes on some genera and species previously cited in the checklist by Buaruang & al. (2017).

Notes

Some genera listed in the checklist for Thailand (Buaruang & al. 2017) have since been shown not to occur in the country and are not included in this key. These include: *Arctomia* Th. Fr.— the Thai species is now placed in *Gabura* (Magain & al. 2020); *Hemithecium* Trevis.—the Thai species are currently classified in *Graphis* (Kalb & al. 2018); *Maronina* Hafellner & R.W. Rogers—the Thai species are currently accepted in *Neoprotoparmelia* (Singh & al. 2018); and *Rostania* Trevis.—the single species recorded from Thailand is now placed in *Collema* (Kosuthova & al. 2019). *Cryptothelium sepultum* (Mont.) A. Massal. is now accepted as *Astrothelium sepultum* Mont. (Lücking & al. 2016c); and *Spilonema* Bornet does not occur in Thailand (Spribille & al. 2014), where the Thai species is now classified in *Erinacellus*. Furthermore, *Arthonia ochrodes* Nyl. ex Willey has been referred to the lichenicolous fungus *Synarthonia* Müll. Arg. However, the Thai material does not agree with the type from Cuba and requires further study (van den Broeck & al. 2018). *Blastenia* A. Massal. is not keyed out, since its presence in Thailand is doubtful, and *B. testaceorufa* (Vain.) Zahlbr. does not belong to the genus as currently circumscribed (Arup & al. 2013). "*Lobariella isidiosa* Moncada & Lücking" was listed in the checklist by error—the material belongs to *Lobaria isidiosa* (Müll. Arg.) Vain., not *Lobariella isidiata* Moncada & Lücking; the genus *Lobariella* Yoshim. does not occur in Thailand. The genus *Sulzbacheromyces,* which has been recorded from Thailand since the publication of the checklist (Suwannarach & al. 2019), is included in this key.

Key to the genera of Thai lichenized fungi

1. Thallus foliose, fruticose, dimorphic or squamulose 2
1. Thallus crustose, leprose, byssoid or filamentous 93

2. Thallus foliose or squamulose 3
2. Thallus fruticose or dimorphic 79

3. Thallus gelatinous, with cyanobacteria, homoiomerous 4
3. Thallus not gelatinous, with green algae or cyanobacteria, heteromerous 7

4. Thallus corticate,
ascospores transversely septate to muriform ..... *Leptogium* (Ach.) Gray
4. Thallus ecorticate, ascospores simple or transversely septate to muriform 5

5. Ascospores simple, thallus leathery, adnate, ≤10 cm wide ..... *Physma* A. Massal.
5. Ascospores transversely septate to muriform,
thallus tightly or loosely adnate to ±cushion-forming 6

6. Thallus foliose, lobes >3 mm wide, not squamulose or subcrustose,
ascospores narrowly ellipsoidal to fusiform,
transversely septate or muriform..... *Collema* Weber ex F.H. Wigg.
6. Thallus smaller, when foliose then lobes <3 mm wide, squamulose, shrubby or
crustose, ascospores transversely septate, thin-walled ..... *Gabura* Adans.
Note: One species known from Thailand: *G. fascicularis* (L.) P.M. Jørg.

7. Thallus squamulose..... 8
7. Thallus foliose 24

8. Ascomata perithecia, located between squamules,
ascospores muriform..... *Agonimia* Zahlbr.
Note: Recent key to the genus available (Breuss 2020).
8. Ascomata an apothecium or thallus sterile 9

9. Apothecia immersed..... 10
9. Apothecia sessile to raised, or thallus sterile..... 11
10. Asci polyspored, ascospores simple,
thallus containing cyanobacteria ..... *Peltula* Nyl.
10. Asci 8-spored, ascospores 1-septate,
thallus containing green algae ..... *Rolfidium* Moberg
Note: One species known from Thailand: *R. coccocarpioides* (Nyl.) Timdal

11. Photobiont a cyanobacterium, apothecia with a thalline margin 12
11. Photobiont a green alga, apothecia lacking a thalline margin or sterile 14

12. Thallus on a distinct blackish hypothallus..... *Lepidocollema* Vain.
12. Thallus lacking a distinct hypothallus, often with lichen substances..... 13

13. Thalline margin of apothecia excluded when mature,
asci with amyloid apical structures,
hymenium I+ red-brown..... *Fuscopannaria* P.M. Jørg.
Note: One species known from Thailand: *F. siamensis* P.M. Jørg. & Wolseley
13. Thalline margin of apothecia prominent and persisting when mature,
asci without amyloid apical structures,
hymenium I+ dark blue..... *Pannaria* Delise ex Bory
Note: One species known from Thailand: *P. dispartita* (Nyl.) Vain.

14. Thallus consisting of small ear-like squamules, with raised margins,
bluish grey ..... *Normandina* Nyl.
Note: One species known from Thailand: *N. pulchella* (Borrer) Nyl.
14. Thallus different..... 15

15. Thallus lacking a prothallus 16
15. Thallus with a well-developed prothallus 21

16. Ascospores brown ..... *Hypoflavia* Marbach
Note: One species known from Thailand: *H. crustosa* Aptroot
16. Ascospores hyaline, or thallus sterile 17

17. Thallus sterile and usually growing on soil or rocks 18
17. Thallus with sessile or stalked apothecia lacking a thalline margin, growing on bark or rocks 19

18. Lobes thick, greenish to greenish gray, usually >1 mm wide primary squamules of *Cladonia* spp.
18. Lobes thin, grayish blue-green to brown, <1 mm wide ..... *Flakea* O.E. Erikss.
Note: One species known from Thailand: *F. papillata* O.E. Erikss.

19. Thallus with stalked, biatorine apothecia, ascospores simple ..... *Gymnoderma* Nyl.
Note: One species known from Thailand: *G. coccocarpum* Nyl.
19. Thallus with sessile, biatorine apothecia 20

20. Saxicolous, ascospores 3-septate ..... *Septotrapelia* Aptroot & Chaves
20. Corticolous, ascospores 1-septate ..... *Eschatogonia* Trevis.

21. Apothecia zeorine, ascospores 1–3-septate ..... *Physcidia* Tuck.
21. Apothecia biatorine 22

22. Ascospores transversely septate, with up to 17 septa ..... *Bacidiopsora* Kalb
22. Ascospores simple to 1-septate 23

23. Ascospores up to 20 µm long ..... *Phyllopsora* Müll. Arg.
Note: Recent key to Asian species available (Kistenich & al. 2019).
23. Ascospores 25–40 µm long ..... *Triclinum* Fée

24. Lower surface of thallus with ±rounded pores, either cyphellae or pseudocyphellae 25
24. Lower surface of thallus lacking cyphellae and pseudocyphellae 29

25. Medulla yellow, lower surface with yellow pseudocyphellae with green algal photobiont ..... *Crocodia* Link
25. Medulla white, lower surface with cyphellae, cyphelloid pores, or yellow or white pseudocyphellae 26

26. Lower surface with pseudocyphellae that lack a distinct margin 27
26. Lower surface with pores with a distinct margin, with either cyphellae or cyphelloid pores 28

27. Thallus of different colors, lower surface more or less tomentose, apothecia laminal, ascospores transversely septate ..... *Pseudocyphellaria* Vain.
27. Thallus containing usnic acid, yellowish green, lower surface not tomentose, apothecia marginal, ascospores simple (green algal photobiont and no cephalodia) ..... *Nephromopsis* Müll. Arg.

28. Lower surface of thallus with cyphelloid pores, thallus containing the gyrophoric acid chemosyndrome ..... *Dendriscosticta* Moncada & Lücking
28. Lower surface of thallus with distinct cyphellae, thallus lacking secondary metabolites ..... *Sticta* (Schreb.) Ach.

29. Thallus yellow to yellow-orange, ascospores simple..... *Candelaria* A. Massal.
NOTE: One species known from Thailand: *C. concolor* (Dicks.) Arnold
29. Thallus of different colors, including yellowish green, but not yellow to yellow-orange 30

30. Lower thallus surface glossy black, erhizinate and not tomentose, lobes hollow..... 31
30. Lower surface of thallus of different colors, mostly rhizinate or tomentose, lobes solid 32

31. Upper surface of thallus perforated, 2–8 ascospores per ascus ..... *Menegazzia* A. Massal.
NOTE: One species known from Thailand: *M. terebrata* (Hoffm.) A. Massal.
31. Upper surface without perforations, 8 ascospores per ascus ..... *Hypogymnia* (Nyl.) Nyl.

32. Thallus containing cyanobacteria as primary photobiont..... 33
32. Thallus containing green algae as primary photobiont, cyanobacteria absent or present as secondary photobiont in cephalodia..... 38

33. Apothecia on lower surface of thallus ..... *Nephroma* Ach.
NOTE: One species known from Thailand: *N. helveticum* Ach.
33. Apothecia laminal or marginal on upper thallus surface, or thallus sterile 34

34. Upper surface of thallus with stiff hairs, or strongly tomentose..... 35
34. Upper surface of thallus different 36

35. Thallus with stiff hairs or strongly tomentose, Pd+ yellow-orange ... *Erioderma* Fée
NOTE: One species known from Thailand: *E. sorediatum* D.J. Galloway & P.M. Jørg.
35. Thallus strongly tomentose, lacking stiff hairs, Pd– ..... *Leioderma* Nyl.
NOTE: One species known from Thailand: *L. sorediatum* D.J. Galloway & P.M. Jørg.

36. Lower surface of thallus ecorticate, with pale to dark veins and conspicuous rhizines..... *Peltigera* Willd.
NOTE: One species known from Thailand: *P. pindarensis* D.D. Awasthi & M. Joshi
36. Lower surface of thallus without veins..... 37

37. Apothecia adnate, proper margin soon becoming excluded, photobiont *Scytonema*, lower surface of thallus with dense rhizines ..... *Coccocarpia* Pers.
37. Apothecia sessile, proper margin persistent, photobiont *Nostoc*, lower surface of thallus with sparse to dense rhizines ..... *Lobaria* (Schreb.) Hoffm.

38. Thallus with pseudocyphellae on the upper surface 39
38. Thallus lacking pseudocyphellae on the upper surface 43

39. Thallus yellowish green, containing usnic acid ..... *Nephromopsis* Müll. Arg.
39. Thallus greenish gray to gray, containing atranorin 40

40. Thallus closely appressed to the substrate by the lower cortex or inconspicuous rhizines 41
40. Thallus loosely attached to the substrate 42

41. Thallus with distinct, linear or reticulate pseudocyphellae, lobes not fusing laterally ..... *Pyxine* Fr.
    Note: Recent key to Thai species is available (Mongkolsuk & al. 2012).
41. Thallus with indistinct pseudocyphellae or pseudocyphellae lacking, lobes often fusing laterally ..... *Dirinaria* (Tuck.) Clem.

42. Thallus with marginal cilia, upper surface finely maculate ..... *Parmotrema* A. Massal.
42. Thallus lacking marginal cilia, pseudocyphellae punctiform ..... *Cetrelia* W.L. Culb. & C.F. Culb.

43. Thallus with bulbate marginal cilia 44
43. Thallus lacking bulbate cilia 45

44. Thallus yellowish green, containing usnic acid ..... *Relicina* (Hale & Kurok.) Hale
44. Thallus grayish green, lacking usnic acid, containing atranorin ..... *Bulbothrix* Hale

45. Thallus yellow-green or greenish yellow to yellowish brown, containing cephalodia, with a non-trebouxioid primary photobiont 46
45. Thallus of different colors, containing a trebouxioid or non-trebouxioid photobiont, lacking cephalodia 47

46. Thallus small-foliose, apothecia with thick thalline margin, ascospores simple, thick-walled with an epispore ..... *Gibbosporina* Elvebakk & al.
    Note: One species known from Thailand: *G. boninensis* (Kurok.) Elvebakk & P.M. Jørg.
46. Thallus larger, ascospores transversely septate, thin-walled ..... *Lobaria* (Schreb.) Hoffm.

47. Thallus containing a non-trebouxioid photobiont, lobes broad, lower surface whitish gray ..... *Ricasolia* De Not.
    Note: One species known from Thailand: *R. discolor* (Bory) Nyl.
47. Thallus containing a trebouxioid photobiont, lobes and lower surface variable 48

48. Upper surface of thallus yellow-green to greenish yellow, containing usnic acid, apothecia with a thalline margin 49
48. Upper surface of thallus whitish, gray, olive-green or brown to blackish brown, lacking usnic acid, apothecia with or without thalline margin 54

49. Thallus with truncated lobe apices, rhizines squarrosely to dichotomously branched ..... *Hypotrachyna* (Vain.) Hale
49. Thallus with rounded or incised lobe apices, rhizines usually simple 50

50. Thallus lobes broad, usually >2 mm wide 51
50. Thallus lobes narrower, <2 mm wide 52

51. Lobes apically rounded, on bark or rocks, loosely adnate,
Thai species sorediate ..... *Flavoparmelia* Hale
Note: One species known from Thailand: *F. caperata* (L.) Hale
51. Lobes ±apically incised, on rocks,
Thai species not sorediate ..... *Xanthoparmelia* (Vain.) Hale

52. Thallus growing on rock ..... *Xanthoparmelia* (Vain.) Hale
52. Thallus growing on bark or wood 53

53. Thallus adnate, lobes sublinear, 0.5–1.5 mm wide, sorediate,
at high altitudes ..... *Parmeliopsis* (Nyl.) Nyl.
Note: One species known from Thailand: *P. ambigua* (Hoffm.) Nyl.
53. Thallus adnate, lobes irregular to linear-elongate, contiguous in the center,
0.5–2 (–3) mm wide ..... *Relicina* (Hale & Kurok.) Hale

54. Thallus with broad lobes, >5 mm wide 55
54. Thallus with narrower lobes, <5 mm wide 57

55. Thallus with cilia in lobe axils, cilia c. 0.5 mm long ..... *Parmelinella* Elix & Hale
55. Thallus eciliate or with longer cilia (0.5–6 mm long) 56

56. Thallus with a broad erhizinate margin, ciliate or eciliate,
chemistry variable ..... *Parmotrema* A. Massal.

56. Thallus erhizinate or with very few scattered rhizines, eciliate,
medulla containing fatty acids ..... *Platismatia* W.L. Culb. & C.F. Culb.
Note: One species known from Thailand: *P. erosa* W.L. Culb. & C.F. Culb.

57. Thallus with cilia at margins (or marginal rhizines that resemble cilia) 58
57. Thallus eciliate 66

58. Medulla at least partly yellow to orange or orange-red 59
58. Medulla white 60

59. Thallus lobes narrow, usually less than 1 mm wide, dark gray to brownish gray,
lacking atranorin ..... *Phaeophyscia* Moberg

59. Thallus lobes 2–4 mm wide, whitish gray,
containing atranorin ..... *Myelochroa* (Asahina) Elix & Hale

60. Thallus lacking a lower cortex 61
60. Thallus with a lower cortex 62

61. Thallus with linear-elongate, often ribbon-like, dichotomously branched lobes,
loosely attached to the substrate ..... *Leucodermia* Kalb
Note: Recent key to Thai species is available (Mongkolsuk & al. 2015).
61. Thallus with suborbicular lobes, attached to the substrate ..... *Polyblastidium* Kalb
Note: Recent key to Thai species is available (Mongkolsuk & al. 2015).

62. Thallus dark gray to brownish gray, lacking atranorin 63
62. Thallus lighter, often whitish gray, containing atranorin 64

63. Lower cortex of thallus prosoplectenchymatous,
lower surface white ..... *Physciella* Essl.
Note: One species known from Thailand: *P. chloantha* (Ach.) Essl.
63. Lower cortex of thallus paraplectenchymatous,
lower surface usually dark ..... *Phaeophyscia* Moberg

64. Thallus lobes short, richly dichotomously branched, lower surface black,
with short, richly dichotomously branched rhizines,
ascospores hyaline, non-septate ..... *Remototrachyna* Divakar & A. Crespo
64. Thallus lobes either suborbicular or orbicular to spreading irregularly,
lower surface pale or brown, with different rhizines,
ascospores brown, 1-septate 65

65. Upper cortex of thallus consisting of periclinal hyphae ..... *Heterodermia* Trevis.
Note: Recent key to Thai species is available (Mongkolsuk & al. 2015).
65. Upper cortex of thallus paraplectenchymatous ..... *Physcia* (Schreb.) Michx.

66. Thallus subfoliose-peltate, monophyllous, on siliceous rocks .... *Rolfidium* Moberg
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Note: One species known from Thailand: *E. schmidtii* (Vain.) T. Sprib. & al.

84. Lichenized with the cyanobacterial genera *Nostoc* or *Scytonema*, thallus shrub-like, richly branched, attached to substrate by a basal holdfast, cortex well developed, apothecia biatorine, mostly lateral, disc pale to dark brown, ascospores simple or 1-septate..... 85

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85. Lichenized with the cyanobacterial genus *Scytonema*..... *Leptogidium* Nyl.
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90. Thallus filamentous, small, consisting of algal filaments of *Trentepohlia* surrounded by fungal hyphae, ascospores 1-septate, hyaline ..... *Coenogonium* Ehrenb.
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99. Lichenized with the cyanobacterial genus *Scytonema* ..... *Leptogidium* Nyl.
NOTE: One species known from Thailand: *L. dendriscum* (Nyl.) Nyl. (Muggia & al. 2011).

100. Thallus gelatinous, epiphytic ..... *Gabura* Adans.
NOTE: One species known from Thailand: *G. fascicularis* (L.) P. M. Jørg.
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109. Thallus with a cortex and roundish soralia,
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Note: One species known from Thailand: *D. thelephora* (Spreng.) Zahlbr.

116. Thallus with chlorococcoid photobiont, prostrate ..... *Agonimia* Zahlbr.
Note: Recent key to the genus available (Breuss 2020).
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135. Asci multispored (> 8 ascospores) 136
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136. Apothecia yellowish green to orange,
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137. Thallus and apothecia K–, containing pulvinic acid derivatives,
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on various substrates.....*Candelariella* Müll. Arg.
Note: One species known from Thailand: *C. reflexa* (Nyl.) Lettau
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144. Hymenial gel and asci strongly amyloid, ascospore wall 1-layered, apothecia disciform ..... *Ochrolechia* A. Massal.
Note: One species known from Thailand: *O. africana* Vain.
144. Hymenial gel not or weakly amyloid, asci amyloid, ascospore wall 1- or 2-layered, apothecia disciform or poriform 145

145. Asci weakly amyloid, with a distinctive ocular chamber, ascospore wall mostly 2-layered, thick, apothecia disciform or poriform ..... *Pertusaria* DC.
145. Asci strongly amyloid, no structures visible, ascospore wall 1-layered, thick or thin, apothecia disciform 146

146. Ascospores thick-walled, usually containing lecanoric acid ..... *Varicellaria* Nyl.
Note: One species known from Thailand: *V. velata* (Turner) I. Schmitt & Lumbsch
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147. Hymenium not or faintly amyloid 148
147. Hymenium amyloid, paraphyses conglutinate 149

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149. Marginal lobes of thallus elongate, thallus subcrustose ..... *Xanthoparmelia* (Vain.) Hale
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150. Hypothecium hyaline or pale yellowish 151
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151. Thallus and apothecia brownish, exciple cupulate, conidia bacilliform, usually containing the alectoronic acid chemosyndrome ..... *Neoprotoparmelia* Garima Singh & al.
Note: Recent key to species available (Singh & al. 2018).
151. Thallus and apothecia not brownish, exciple annulate, conidia filiform, alectoronic acid chemosyndrome absent ..... *Lecanora* Ach.
Note: Recent key to Thai species available (Papong & Lumbsch 2011).

152. Hymenium purple-violet, apothecial discs black ..... *Tephromela* M. Choisy
152. Hymenium hyaline to pale yellowish, discs of various colors, only rarely blackish brown 153

153. Conidia filiform. ..... *Lecanora* Ach.
Note: Recent key to Thai species available (Papong & Lumbsch 2011).
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154. Hymenium not or faintly amyloid, asci faintly amyloid 155
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156. Thallus containing stictic acid. ..... *Parainoa* Resl & T. Sprib.
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156. Thallus containing the gyrophoric acid chemosyndrome ..... *Trapeliopsis* Hertel & Gotth. Schneid.
Note: One species known from Thailand: *T. viridescens* (Schrad.) Coppins & P. James

157. Thallus byssoid, white to pale gray, ecorticate. ..... *Crocynia* (Ach.) A. Massal.
Note: Recent key to species available (Aptroot & Cáceres 2014a).
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158. Thallus growing on rock. 159
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159. Asci of the *Lecanora*-type. ..... *Ramboldia* Kantvilas & Elix
Note: Recent key to Thai species available (Kalb & al. 2009).
159. Asci of the *Porpidia*-type ..... *Porpidia* Körb.
Note: One species known from Thailand: *P. albocaerulescens* (Wulfen) Hertel & Knoph

160. Thallus with stalked sporodochia and red pigments ... *Sprucidea* M. Cáceres & al.
Note: One species known from Thailand: *S. penicillata* (Aptroot & al.) M. Cáceres & al. (Cáceres & al. 2017).
160. Thallus lacking sporodochia, with or without pigment; if pigmented restricted to medulla, and yellowish to orange, not red 161

161. Asci without a distinct tubular structure in the tholus, thallus usually with warts ..... *Malmidea* Kalb & al.
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161. Asci of the *Lecanora*-type. 162

162. Apothecia over 0.5 mm in diam., hypothecium hyaline ..... *Ramboldia* Kantvilas & Elix
Note: Recent key to Thai species available (Kalb & al. 2009).

162. Apothecia small, under 0.5 mm in diam., hypothecium hyaline or pigmented 163

163. Apothecial margin entire, paraphyses unbranched, hypothecium dark brown, ascospores thin-walled ..... *Punctonora* Aptroot
NOTE: One species known from Thailand: *P. nigropulvinata* Aptroot

163. Apothecial margin ragged, paraphyses branched, hypothecium hyaline, ascospores thick-walled ..... *Traponora* Aptroot
NOTE: Recent key to species available (Aptroot 2009).

164. Ascospores polarilocular, with 2 or more locules 165

164. Ascospores transversely septate to muriform, ascospore wall various 166

165. Ascospores usually with 2 locules, asci of *Teloschistes*-type, 8-spored ..... *Caloplaca* Th. Fr.

165. Ascospores with more than 2 locules, asci of *Letrouitia*-type, 2–8-spored ..... *Letrouitia* Hafellner & Bellem.

166. Ascospores 1-septate 167

166. Ascospores with 3 or more transverse septa, or muriform 171

167. Hymenium inspersed with oil droplets, ascospores relatively thick-walled ..... *Megalospora* Meyen

167. Hymenium clear, ascospores thick- or thin-walled 168

168. Asci with 2 ascospores, more than 40 µm long ..... *Lopezaria* Kalb & Hafellner

168. Asci usually with more ascospores, usually less than 40 µm long 169

169. Asci thin-walled, non-amyloid, hamathecium weakly amyloid ..... *Absconditella* Vězda
NOTE: One species known from Thailand: *A. delutula* (Nyl.) Coppins & H. Kilias

169. Asci with thickened apex, amyloid, hamathecium amyloid 170

170. Asci of *Catillaria*-type, paraphyses with distinct pigment caps, ascospores <20 µm long ..... *Catillaria* A. Massal.

170. Asci of *Lecanora*-type, paraphyses lacking distinct caps, ascospores >20 µm long ..... *Megalaria* Hafellner
NOTE: One species known from Thailand: *M. laureri* (Hepp ex Th. Fr.) Hafellner

171. Hymenium non-amyloid 172

171. Hymenium amyloid or hemiamyloid 173

172. Paraphyses richly branched and anastomosing ..... *Gyalideopsis* Vězda
NOTE: Recent key to species available (Xavier-Leite & al. 2018).

172. Paraphyses simple ..... *Gyalidea* Lettau ex Vězda
NOTE: One species known from Thailand: *G. luzonensis* (Kalb & Vězda) Aptroot & Lücking

173. Ascospores muriform 174

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174. Apothecia K+ violet, containing anthraquinones..... 175

175. Thallus whitish or gray, lacking anthraquinones,
asci 1 (–2)-spored ..... *Brigantiaea* Trevis.
175. Thallus yellowish, containing anthraquinones,
asci 2–8-spored ..... *Letrouitia* Hafellner & Bellem.

176. Apothecia lecanorine or immersed in verrucae 177
176. Apothecia biatorine or lecideine..... 179

177. Apothecia lecanorine, discs red, K+ red,
ascospores thin-walled.....*Haematomma* A. Massal.
177. Apothecia immersed in verrucae, discs not pigmented 178

178. Paraphyses simple to apically sparingly branched,
asci with weakly amyloid tholus, ascospores
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178. Paraphyses slightly branched, asci with an amyloid tholus, ascospores
relatively thin-walled, spiraled, containing depsides..... *Loxospora* A. Massal.
Note: One species known from Thailand: *L. lecanoriformis* Lumbsch & al.

179. Exciple poorly developed, consisting of paraphysis-like hyphae,
asci of *Lecanora*-type, ascospores twisted..... *Scoliciosporum* A. Massal.
Note: One species known from Thailand: *S. umbrinum* (Ach.) Lojka
179. Exciple well developed, ascospores and asci variable..... 182

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180. Thallus lacking stalked soralia..... 181

181. Asci of *Catillaria*-type, hypothecium dark,
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181. Asci of *Bacidia*-type, hypothecium hyaline to pigmented,
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182. Mazaedium present, asci prototunicate, ascospores brown 183
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Note: Recent key to species available (Singh & Singh 2017).
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187. Apothecia with a thick,
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Note: Recent key to species available (Ertz & al. 2011).
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Note: Recent key to species available (Singh and Singh 2017).

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ascomata orbicular, urceolate, apothecioid or perithecioid 190
189. Paraphyses more or less branched and often anastomosing, rarely simple,
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191. Ascospores non-septate, apothecia immersed in the thallus ..... *Ionaspis* Th. Fr.
Note: One species known from Thailand: ***Ionaspis aptrootii*** Poengs. & Lumbsch,
nom. nov., MB 835127; ≡ *Ionaspis tropica* Aptroot, Biblioth. Lichenol. 64: 73. 1997,
nom. illeg., non *Ionaspis tropica* Riddle (Britton & Millspaugh 1920).
191. Ascospores transversely septate to muriform 192

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Note: Recent key to species available (Staiger 2002).
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197. Apothecia with recurved margins, ascospores non-amyloid ..... *Astrochapsa* Parnmen & al.
Note: Recent key to species available (Borgato & Ertz 2018).

197. Apothecial margins not or slightly recurved, with striate exciple filling the disc ..... *Pseudotopeliopsis* Parnmen & al.
Note: One species known from Thailand: *P. laceratula* Müll ArgParnmen & al.

198. Exciple indistinct, periphysoids lacking..... *Gyalecta* Ach. [= *Cryptolechia* A. Massal.]

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199. Thallus indistinct, apothecia immersed to erumpent, asci thin-walled throughout, ascospores 1-septate to muriform ..... *Ramonia* Stizenb.
Note: One species known from Thailand: *R. minima* J. Kalb & Kalb (Kalb & Kalb 2017).

199. Thallus thin, gray to olive-gray, apothecia sessile to subimmersed, asci thin-walled, with a thickened apex, ascospores transversely septate (to muriform)..... *Topeliopsis* Kantvilas & Vězda
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Note: One species known from Thailand: *F. argentea* (Müll. Arg.) Rivas Plata & Lücking

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202. Apothecia with a more or less fused exciple and lacking a distinct split between exciple and thalline margin 205

203. Thallus ecorticate or with a loose cortex, if with dense cortex then lacking stictic acid ..... *Thelotrema* Ach.
Note: Recent key to species available (Rivas Plata & al. 2010).

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Note: One species known from Thailand: *A. terebrans* (Nyl.) I. Medeiros & al.

205. Apothecial discs more or less concealed by the incurved, denticulate margins, paraphyses apically not distinctly thickened. . . . . *Topeliopsis* Kantvilas & Vězda
Note: One species known from Thailand: *T. darlingtonii* Frisch & Kalb

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206. Apothecia with a fused exciple, cortex and chemistry variable 207

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207. Thallus ecorticate or partly corticate, matt 209

208. Apothecia with recurved margins, ascospores brown, amyloid. . . . . *Nitidochapsa* Parnmen & al.
Note: Recent key to species available (Poengsungnoen & al. 2014).

208. Apothecial margins not or slightly recurved, with striate exciple filling the disc . . . . . *Pseudotopeliopsis* Parnmen & al.
Note: one species known from Thailand: *P. laceratula* (Müll. Arg.) Parnmen & al.

209. Exciple more or less brown, ascospores amyloid . . . . . *Pseudochapsa* Parnmen & al.

209. Exciple hyaline to yellowish, ascospores non-amyloid . . . . . *Chapsa* A. Massal.
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210. Apothecia solitary, lacking a columella 211

210. Apothecia solitary or pseudostromatic, with a columella or columella-like sterile tissue in the hymenium 217

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212. Apothecia emergent to sessile, hymenium inspersed or rarely clear, exciple carbonized 213

212. Apothecia immersed to sessile, hymenium mostly clear, rarely inspersed, exciple hyaline to brownish. 214

213. Apothecia with a yellow to orange disc, hymenium inspersed with small oil droplets, ascospores ellipsoid to broadly ellipsoid, containing protocetraric acid . . . . . *Ampliotrema* Kalb

213. Apothecia lacking pigments, hymenium clear or inspersed, ascospores narrowly fusiform to cylindrical, lacking secondary metabolites . . . . . *Trinathotrema* Lücking & al.
Note: Recent key to species available (Kalb & Kalb 2017).

214. Apothecia immersed, exciple prosoplectenchymatous, chemistry variable but psoromic acid common ..... *Myriotrema* Fée
NOTE: Recent key to species available (Lücking & al. 2016b).

214. Apothecia immersed to sessile, exciple paraplectenchymatous, chemistry variable but psoromic acid absent and stictic acid common 215

215. Apothecia immersed with a pore-like opening, ascospores hyaline, non-amyloid, thallus with prosoplectenchymatous cortex ..... *Wirthiotrema* Rivas Plata & al.

215. Apothecia immersed to sessile, with a broader opening, ascospores brown, rarely hyaline, non- or weakly amyloid, thallus ecorticate or with a weakly developed cortex..... 216

216. Young ascospores thick-walled, thallus loosely attached to substrate, with large clusters of columnar crystals, medulla with red crystals ..... *Sanguinotrema* Lücking
NOTE: One species known from Thailand: *S. wightii* (Taylor) Lücking.

216. Young ascospores thin-walled, thallus firmly attached to the substrate, with irregularly dispersed crystals, medulla lacking red crystals..... *Leucodecton* A. Massal.

217. Ascospores diamond-shaped, non-amyloid, exciple carbonized ..... *Clandestinotrema* Rivas Plata & al.
NOTE: One species known from Thailand: *C. clandestinum* (Ach.) Rivas Plata & al.

217. Ascospores not diamond-shaped, amyloid or non-amyloid, exciple hyaline to carbonized 218

218. Columella broad-based, carbonized, thallus ecorticate or with weakly developed cortex..... *Melanotrema* Frisch

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219. Apothecia pseudostromatic, columella absent.... *Compositrema* Rivas Plata & al.
NOTE: One species known from Thailand: *C. thailandicum* Rivas Plata & al.

219. Apothecia solitary, columella present 220

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221. Apothecia uncarbonized or weakly carbonized, margins thick, discs usually pruinose ..... *Stegobolus* Mont.
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221. Apothecia distinctly carbonized, margins thin, discs mostly epruinose..... *Rhabdodiscus* Vain.

222. Exciple hyaline, pseudocolumella present, ascospores relatively small..... *Glaucotrema* Rivas Plata & Lumbsch
NOTE: Recent key to species available (Lücking & al. 2016b).

222. Exciple hyaline to carbonized, columella present, ascospores of various sizes. ..... *Ocellularia* G. Mey.
Note: Recent key to Thai species available (Sutjaritturakan & Kalb 2015).

223. Ascomata not well defined, asci weakly aggregated in clusters or scattered, broadly clavate 224
223. Ascomata present, orbicular, asci clavate or cylindrical, ascospores various ... 225

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226. Ascomata lecideine, paraphyses weakly anastomosing, ascospores multi-septate, acicular, sometimes separating into part-spores in the ascus ..... *Bactrospora* A. Massal.
Note: Recent key to species available (Sobreira & al. 2015)
226. Ascomata with pseudothalline margin, paraphyses simple, ascospores not separating into part-spores..... *Graphidastra* (Redinger) G. Thor

227. Thallus byssoid ..... *Dichosporidium* Pat.
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227. Thallus crustose. 228

228. Ascomata perithecioid, in stromata ..... *Chiodecton* Ach.
Note: Key to species available (Thor 1990).
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229. Exciple containing crystals, asci clavate, apothecial discs often pruinose ..... *Cresponea* Egea & Torrente
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Note: Recent key to species available (Thor 1990).

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234. Ascomatal margins distinct, asci cylindrical to clavate 236

235. Ascospores transversely septate ..... *Arthonia* Ach.
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236. Ascomata with a pseudothalline margin, orbicular to slightly lirellate, ascospores biclavate ..... *Graphidastra* (Redinger) G. Thor
236. Ascomata without a pseudothalline margin, lirellate, ascospores various 237

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Note: Recent key to species available (Seavey & Seavey 2014).
237. Ascomata sessile, exciple and/or hypothecium pigmented 238

238. Ascomata ellipsoid to shortly lirelliform, asci cylindrical, without apical thickening ..... *Lecanographa* Egea & Torrente
Note: One species known from Thailand: *L. atropunctata* Sparrius & al.
238. Ascomata lirelliform, asci clavate to cylindrical, apically thickened ..... *Opegrapha* Ach.

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240. Exciple not carbonized 241
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244. Thallus ecorticate, whitish gray, discs whitish-pruinose ..... *Diorygma* Eschw.
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Note: Recent key to Thai species available (Kalb & al. 2018).

245. Apothecial discs brown-pruinose ..... *Glyphis* Ach.
Note: Recent key to species available (Staiger 2002).
245. Apothecial discs epruinose or with whitish or yellowish pruina 246

246. Thallus containing lecanoric acid, C+ red, apothecial discs heavily whitish-pruinose ..... *Dyplolabia* A. Massal.
Note: Recent key to species available (Kalb & al. 2016b).
246. Thallus lacking substance or containing other substances, apothecial discs epruinose or pruinose 247

247. Periphysoids warty, labia covered by whitish pruina, ascospores non- or weakly amyloid ..... *Carbacanthographis* Staiger & Kalb
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247. Periphysoids not warty, labia exposed or partly covered by thallus, ascospores strongly amyloid ..... *Allographa* Chevall. & *Graphis* Adans.
NOTE: Recent key to Thai species available (Kalb & al. 2018).

248. Ascomata not carbonized 249
248. Ascomata at least partly carbonized 252

249. Ascospores non-amyloid, walls not thickened ..... *Phaeographopsis* Sipman
NOTE: Recent key to species available (Kalb & Kalb 2017).
249. Ascospores amyloid or non-amyloid, walls thickened 250

250. Ascomata stromatoid ..... *Creographa* A. Massal.
NOTE: One species known from Thailand: *C. subbrasiliensis* Sutjaritt. & Kalb
250. Ascomata not in stromata 251

251. Ascomata with distinct labiae covering the apothecial discs ..... *Pallidogramme* Staiger & al.
251. Ascomata with indistinct labiae and exposed apothecial discs ..... *Phaeographis* Müll. Arg. [= *Gymnographa* Müll. Arg.]

252. Ascomata stromatoid ..... *Sarcographa* Fée
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253. Hypothecium not carbonized, exciple carbonized ..... *Platygramme* Fée
NOTE: Recent key to Thai species available (Kalb & Kalb 2017).
253. Hypothecium carbonized 254

254. Labiae indistinct, ascospores transversely septate ..... *Leiorreuma* Eschw.
254. Labiae distinct, ascospores muriform 255

255. Apothecial discs pruinose, hymenium not red ..... *Thecaria* Fée
NOTE: One species known from Thailand: *T. quassiicola* Fée
255. Apothecial discs epruinose, hymenium dark red ..... *Pliariona* A. Massal.
NOTE: One species known from Thailand: *P. montagnei* (Bosch) A. Massal.

256. Ascospores non-septate, hyaline 257
256. Ascospores septate, hyaline or brown 260

257. Paraphyses present, periphyses absent, ascospores over 30 µm long, thick-walled ..... *Pertusaria* DC.
257. Paraphyses absent, periphyses present, ascospores variable 258

258. Ascospores over 30 µm long, thick-walled, on bark ..... *Coccotrema* Müll. Arg.
258. Ascospores smaller, thin-walled, on rocks 259

259. Thallus endolithic, perithecial involucrellum with star-shaped aperture, perithecia immersed. ..... *Bagliettoa* A. Massal.
NOTE: One species known from Thailand: *B. baldensis* (A. Massal.) Vězda

259. Thallus epi- or endolithic, perithecial involucrellum lacking star-shaped aperture, perithecia sessile or rarely immersed. ..... *Verrucaria* Schrad.
NOTE: One species known from Thailand: *V. muralis* Ach.

260. Mazaedium present, asci prototunicate, ascospores brown 261

260. Mazaedium absent, asci uni- or bitunicate, ascospores hyaline or brown 262

261. Ascomata with poriform opening disc, photobiont trebouxioid ... *Pyrgidium* Nyl.
NOTE: One species known from Thailand: *P. montellicum* (Beltr.) Tibell

261. Ascomata with widely exposed disc, photobiont *Trentepohlia*. ..... *Pyrgillus* Nyl.
NOTE: Recent key to species available (Singh & Singh 2017).

262. Paraphyses or other interascal hyphae absent, ascospores muriform 263

262. Paraphyses or other interascal hyphae present, ascospores various. 264

263. Hymenium lacking algae, usually on bark ..... *Agonimia* Zahlbr.
NOTE: Recent key to the genus available (Breuss 2020).

263. Hymenium with algae, on soil and calcareous rocks ..... *Endocarpon* Hedw.

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264. Ascospores hyaline 273

265. Asci unitunicate, paraphyses simple to sparingly branched, periphysoids, if present, going down to the hymenium 266

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NOTE: Recent key to species available (Rivas Plata & al. 2010).

266. Photobiont trentepohlioid, on various substrates ..... Genera with perithecioid apothecia – see 188

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267. Paraphyses strongly branched and anastomosing 272

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268. Ascomata solitary 270

269. Asci broadly clavate, thick-walled, ascospores muriform ..... *Mycoporum* Flot. ex Nyl.
NOTE: One species known from Thailand: *M. compositum* (A. Massal.) R.C. Harris

269. Asci cylindrical to clavate, only apically thickened, ascospores transversely septate to muriform ..... *Pyrenula* Ach.
NOTE: Recent key to species available (Aptroot 2012).

270. Ascospores red-brown with rounded lumina ..... *Lithothelium* Müll. Arg.
NOTE: Recent key to species available (Aptroot 2006).

270. Ascospores gray to brown, not red-brown 271

271. Ascospores distoseptate, transversely septate to muriform..... *Pyrenula* Ach.
Note: Recent key to species available (Aptroot 2012).
271. Ascospores euseptate, muriform..... *Anthracothecium* Hampe ex A. Massal.
Note: Recent key to species available (Aptroot 2012).

272. Ascospores small (less than 20 µm long), ascomata exposed, black ..... *Bogoriella* Zahlbr.
Note: Recent key to species available (Aptroot & Lücking 2016).
272. Ascospores larger, ascomata covered at least in part by the thallus ..... *Architrypethelium* Aptroot
Note: One species known from Thailand: *A. murisporum* Luangsuph. & al.

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273. Asci bitunicate..... 277

274. Photobiont trebouxioid, asci thick-walled..... *Aspidothelium* Vain.
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275. Asci thick-walled, periphysoids, if present, going down to the hymenium ..... Genera with perithecioid apothecia – see 189
275. Asci thin-walled, apically with refractive ring 276

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278. Ascomata stromatoid, ascospores muriform ..... *Mycoporum* Flot. ex Nyl.
Note: One species known from Thailand: *M. compositum* (A. Massal.) R.C. Harris
278. Ascomata solitary, ascospores transversely septate to submuriform.... *Strigula* Fr.

279. Hamathecium pseudoparenchymatous..... *Tomasellia* A. Massal.
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280. Ascospores 1-septate 281
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281. Ascospores small to medium-sized (up to 50µm long), with thin walls and septa, thallus usually thin ..... *Anisomeridium* (Müll. Arg.) M. Choisy
281. Ascospores large (above 50µm long), with thick walls and septa, thallus thick ..... *Megalotremis* Aptroot

282. Ascospores filiform, transversely septate..... *Celothelium* A. Massal.
Note: One species known from Thailand: *C. aciculiferum* (Nyl.) Vain.
282. Ascospores fusiform to ellipsoid, transversely septate to muriform 283

283. Ascospores euseptate, muriform. . . . . *Julella* Fabre
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283. Ascospores distoseptate, transversely septate to muriform. 284

284. Paraphyses simple . . . . . *Lithothelium* Müll. Arg.
Note: Recent key to species available (Aptroot 2006).

284. Paraphyses strongly branched and anastomosing 285

285. Thallus ecorticate, ascomata exposed, dark-pigmented 286

285. Thallus corticate, ascomata at least in part covered by thallus 288

286. Paraphyses basally thickened, not anastomosing . . *Constrictolumina* Lücking & al.
Note: One species known from Thailand: *C. cinchonae* (Ach.) Lücking & al.

286. Paraphyses thickness uniform, anastomosing 287

287. Ascospore lumina angular,
endospore thin. . . . . *Polymeridium* (Müll. Arg.) R.C. Harris
Note: Recent key to species available (Aptroot & Cáceres 2014b).

287. Ascospores with diamond-shaped lumina,
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288. Ascospores with rectangular to oval lumina, transversely septate. 289

288. Ascospores with diamond-shaped lumina, transversely septate to muriform . . 291

289. Ascomata in brown-black, sessile stromata,
ascospores 3–9-septate, up to 40 µm long. . . . . *Bathelium* Ach.
Note: Recent key to species available (Aptroot & Lücking 2016).

289. Ascomata in variously colored stromata or solitary,
ascospores (5–)9–19-septate, over 40 µm long. 290

290. Ascomata immersed-erumpent, solitary to aggregated,
pigments absent. . . . . *Viridothelium* Lücking & al.
Note: One species known from Thailand: *V. virens* (Tuck. ex Michener) Lücking & al.

290. Ascomata in erumpent to prominent pseudostromata,
often pigmented. . . . . *Trypethelium* Spreng.
Note: Recent key to species available (Aptroot & Lücking 2016).

291. Ascospores transversely septate 292

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292. Ascospores very large, 3(–5)-septate, with a reduced
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Note: One species known from Thailand: *A. murisporum* Luangsuph. & al.

292. Ascospores usually small to medium-sized. 293

293. Ascomata prominent to sessile, fully exposed and black, solitary, lacking
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293. Ascomata immersed to prominent or in immersed to sessile stromata, at least partly covered by thallus, often with yellow-orange pigment ..... *Astrothelium* Eschw.

294. Ascomata in prominent stromata filled with yellow-orange pigments ..... *Bathelium* Ach.
Note: Recent key to species available (Aptroot & Lücking 2016).

294. Ascomata immersed to sessile or in immersed to sessile stromata, at least partly covered by thallus, with or without pigments 295

295. Ascomata in large, prominent to sessile stromata, red or yellow-orange warts ..... *Marcelaria* Aptroot & al.
Note: Recent key to species available (Aptroot & Lücking 2016).

295. Ascomata immersed to prominent or in immersed to sessile stromata, lacking pigments or with a thin pigment layer ..... *Astrothelium* Eschw. & *Viridothelium* Lücking & al.
Note: Recent key to species available (Aptroot & Lücking 2016).

296. Ascomata not well defined, asci weakly aggregated in clusters or scattered, broadly clavate, ascospores muriform ..... *Cryptothecia* Stirt.

296. Ascomata well defined, either apothecia or perithecia 297

297. Ascomata with open discs (apothecia) 298

297. Ascomata opening with a small pore (perithecia) 329

298. Apothecia lirellate 299

298. Apothecia orbicular 303

299. Apothecial margin carbonized, lacking algae 300

299. Apothecial margin not carbonized, containing algae 301

300. Photobiont trentepohlioid, asci bitunicate ..... *Opegrapha* Ach.

300. Photobiont chlorococcoid, asci unitunicate ..... *Aulaxina* Fée
Note: Recent key to species available (Lücking 2008).

301. Ascospores muriform ..... *Gyalectidium* Müll. Arg.

301. Ascospores transversely septate 302

302. Apothecial margin well-developed, ascospores 3–15-septate ..... *Enterographa* Fée
Note: Recent key to species available (Seavey & Seavey 2014).

302. Apothecial margin reduced, ascospores 1–2-septate ..... *Arthonia* Ach.

303. Photobiont trentepohlioid 304

303. Photobiont chlorococcoid 307

304. Ascomata adnate and spot-like, asci obovate to globose, bitunicate ..... *Eremothecella* Syd. & P. Syd.
Note: Recent key to species available (Jagadesh Ram & Sinha 2019).

304. Ascomata immersed to erumpent or sessile, asci cylindrical to clavate, uni- or bitunicate 305

305. Apothecial discs dark gray to black, asci bitunicate, paraphyses anastomosing ..... *Mazosia* A. Massal.
Note: Recent key to species available (Lücking 2008).

305. Apothecial discs yellowish green, light gray or orange-red, asci unitunicate, paraphyses not anastomosing 306

306. Apothecial margins recurved, prominent, ascospores transversely septate to muriform .*Chroodiscus* (Müll. Arg.) Müll. Arg.
Note: Recent key to species available (Papong & al. 2009).

306. Apothecia biatorine, margins not recurved, ascospores 1-septate ..... *Coenogonium* Ehrenb.
Note: Recent key to Thai species available (Kalb & al. 2016a).

307. Hymenium non-amyloid 308

307. Hymenium amyloid 318

308. Thallus corticate 309

308. Thallus ecorticate 310

309. Apothecia pale yellowish, exciple hyaline ..... *Asterothyrium* Müll. Arg.
Note: Recent key to species available (Lücking 2008).

309. Apothecia black, exciple at least partly carbonized ..... *Psorotheciopsis* Rehm
Note: One species known from Thailand: *P. patellarioides* (Rehm) R. Sant.

310. Sterile setae present 311

310. Sterile setae absent but hyphophores often present 312

311. Sterile setae pale ..... *Aderkomyces* Bat.

311. Sterile setae black ..... *Tricharia* Fée

312. Apothecial margin dark brown to black, exciple carbonized ..... *Aulaxina* Fée
Note: Recent key to species available (Lücking 2008).

312. Apothecial margin pale, exciple not carbonized 313

313. Proper exciple well-developed, covered by a cartilaginous layer 314

313. Proper exciple reduced, with a thalline margin or immersed in thallus 315

314. Paraphyses unbranched, hyphophores absent .. *Phyllogyalidea* Lücking & Aptroot
Note: One species known from Thailand: *P. epiphylla* (Vězda) Lücking & Aptroot

314. Paraphyses branched, hyphophores common ..... *Gyalideopsis* Vězda
Note: Recent key to species available (Xavier-Leite & al. 2018).

315. Hyphophores squamiform, ascospores muriform ..... *Gyalectidium* Müll. Arg.

315. Hyphophores setiform 316

316. Apothecia adnate ..... *Echinoplaca* Fée
Note: Recent key to species available (Lücking 2008).

316. Apothecia immersed-erumpent 317

317. Hyphophores pale,
ascospores transversely septate to muriform ..... *Calenia* Müll. Arg.
317. Hyphophores reddish brown,
ascospores 1–3-septate ..... *Rolueckia* Papong & al.
Note: One species known from Thailand: *R. siamensis* Papong & al.

318. Ascospores 1-septate ..... *Fellhanera* Vězda
318. Ascospores with more than 1 septum 319

319. Ascospores transversely septate 320
319. Ascospores muriform 328

320. Ascospores narrowly cylindrical to filiform ..... *Bacidina* Vězda
Note: One species known from Thailand: *B. pallidocarnea* (Müll. Arg.) Vězda
320. Ascospores ellipsoid to cylindrical 321

321. Apothecial margin composed of loosely interwoven hyphae .... *Byssoloma* Trevis.
321. Apothecial margin different 322

322. Exciple with crystals 323
322. Exciple lacking crystals 325

323. Conidia produced in campylidia ..... *Badimia* Vězda
Note: One species known from Thailand: *B. multiseptata* Papong & Lücking
323. Conidia produced in pycnidia 324

324. Apothecial margin distinct, whitish, conidia ellipsoid-fusiform ..... *Eugeniella* Lücking & al.
Note: One species known from Thailand: *E. micrommata* (Kremp.) Lücking & al.
324. Apothecial margin thin, gray, conidia pyriform ..... *Fellhanera* Vězda

325. Conidia produced in pycnidia 326
325. Conidia produced in campylidia 327

326. Apothecia sessile ..... *Fellhanera* Vězda
326. Apothecia adnate and spot-like ..... *Byssolecania* Vain.
Note: Recent key to species available (Lücking 2008).

327. Apothecial discs black, hypothecium brown, K+ purple ..... *Tapellaria* Müll. Arg.
Note: One species known from Thailand: *T. nigrata* (Müll. Arg.) R. Sant.
327. Apothecial discs grayish brown, hypothecium brown, K– ..... *Calopadia* Vězda
Note: Recent key to species available (Lücking 2008).

328. Thallus verrucose, conidia non-septate ..... *Sporopodium* Mont.
328. Thallus smooth, conidia multi-septate ..... *Lasioloma* R. Sant.
Note: One species known from Thailand: *L. phycophilum* (Vain.) R. Sant.

329. Asci unitunicate 330
329. Asci bitunicate 332

330. Perithecia white to pale pink, photobiont trebouxioid ..... *Aspidothelium* Vain.
330. Perithecia yellowish to green, brown or black, photobiont trentepohlioid 331

331. Perithecia glabrous or, if hairy, then involucrellum yellowish to brown *Porina* Ach.
331. Perithecia with black hairs or spines, involucrellum mostly pigmented ..... *Trichothelium* Müll. Arg.

332. Paraphyses absent in perithecia ..... *Microtheliopsis* Müll. Arg.
Note: One species known from Thailand: *M. uleana* Müll. Arg.
332. Paraphyses present in perithecia..... 333

333. Paraphyses unbranched or slightly branched apically, photobiont *Cephaleuros* or *Phycopeltis*..... 334
333. Paraphyses branched, photobiont various..... 337

334. Perithecial wall not carbonized..... *Puigariella* Speg.
Note: One species known from Thailand: *P. nemathora* (Mont.) S.H. Jiang & al.
334. Perithecial wall at least partially carbonized..... 335

335. Thallus supracuticular, photobiont *Phycopeltis*..... *Phylloporis* Clem.
Note: Recent key to species available (Jiang & al. 2020).
335. Thallus subcuticular, photobiont *Cephaleuros* or *Trentepohlia*..... 336

336. Thallus olive-brown to dark green, perithecia covered by thin thallus layer around ostiolum..... *Racoplaca* Fée
Note: Recent key to species available (Jiang & al. 2020).
336. Thallus bright green to grey-green, perithecia black, not covered by thallus ..... *Strigula* Fr.

337. Pycnidia setose, conidia in rectangular packages..... *Caprettia* Bat. & H. Maia
337. Pycnidia globose to conical, conidia in irregular masses ..... *Anisomeridium* (Müll. Arg.) M. Choisy

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Dictyostelids from Jilin Province, China, 4

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Abstract—*Dictyostelium quercibrachium* and *D. crassicaule* were isolated from samples of soil collected on Changbai Mountain, Jilin Province, China. *Dictyostelium quercibrachium* represents a new record from China; and *D. crassicaule*, represents a new record from Jilin Province. Descriptions and illustrations based on these isolates are provided.

Key words—cellular slime molds, *Dictyosteliaceae*, *Mycetozoa*, taxonomy

Introduction

Dictyostelid cellular slime molds (dictyostelids), are ideal organisms for investigating problems in genetics, cytology, and developmental biology because of their unique macroscopic characteristics and life cycles. These organisms are primary inhabitants of soil and play an essential role in maintaining the balance between bacteria and other soil organisms, because they feed mostly on bacteria (Singh 1947; Cavender & Raper 1965a,b; Raper 1973, 1984). At present, about 150 species have been identified, mostly based on a traditional morphological classification system in which

dictyostelids are distributed among four genera based on differences in sorophore structure and branching patterns, but also on a new classification based on unique 18S rRNA sequence signatures (Kirk & al. 2008; Sheikh & al. 2018).

Jilin Province is situated in China's temperate zone and is characterized by a monsoon climate (Liu & Li 2014). Previously, a total of 18 dictyostelids species have been reported from Jilin Province (He & Li 2008; Liu & Li 2014, 2017; Liu & al. 2019). In this study, we report two additional species in *Dictyostelium*, one for the first time from China, and the other for the first time from Jilin Province.

Materials & methods

Samples of soil were collected on Changbai Mountain, Jilin Province in 2014. Each sample consisted of 20–30 g of soil and was placed in a sterile whirl-pack plastic bag and returned to the laboratory for isolation of dictyostelids according to Cavender & Raper (1965a), with some minor modifications outlined by Liu & al. (2019). Each isolate recovered from one of the plates was purified and cultivated for taxonomic studies, with an identification made using morphological descriptions (Raper 1984) and molecular characteristics (Sheikh & al. 2018). Life cycle stages were observed under a Zeiss Axio Zoom V16 dissecting microscope with a 1.5× objective and a 10× ocular. Sorocarps were mounted in water on slides for observation and measurements of spores, sorophores, and sorocarps using a Zeiss Axio Imager A2 light microscope mounted with 10× ocular and 10, 40, and 100× (oil) objectives. Photographs were taken with Zeiss Axiocam 506 color microscope camera. Spores from these isolates were frozen in HL 5 media (Cocucci & Sussman 1970) and stored at −80 °C in the herbarium of the Mycological Institute of Jilin Agricultural University, Changchun, China (HMJAU).

Taxonomy

Dictyostelium quercibrachium Cavender, S.L. Stephenson, J.C. Landolt & Vadell, New Zealand J. Bot. 40: 258. 2002. PLATE 1A–D

When cultured at 23 °C on non-nutrient agar with *E. coli*, sorocarps clustered or solitary, often twisted, unbranched or branched, normally 1.9–4.5 mm long. Sorophore colorless, robust, stout, tapering from bases to tips, consisting of one tier of cells in the terminus, and becoming coremiform at the lower part when clustered and aged. Tips capitate, bases clavate to round. Branches *Quercus*-like, twisted or sometimes recurved, tapering from bases to tips, with small sori. Terminal sori white, globose, commonly 130–290 μm diam. Spores hyaline, elliptical, 4.6–7.6 × 2.9–3.9 μm. Aggregations with radiate flattened streams.

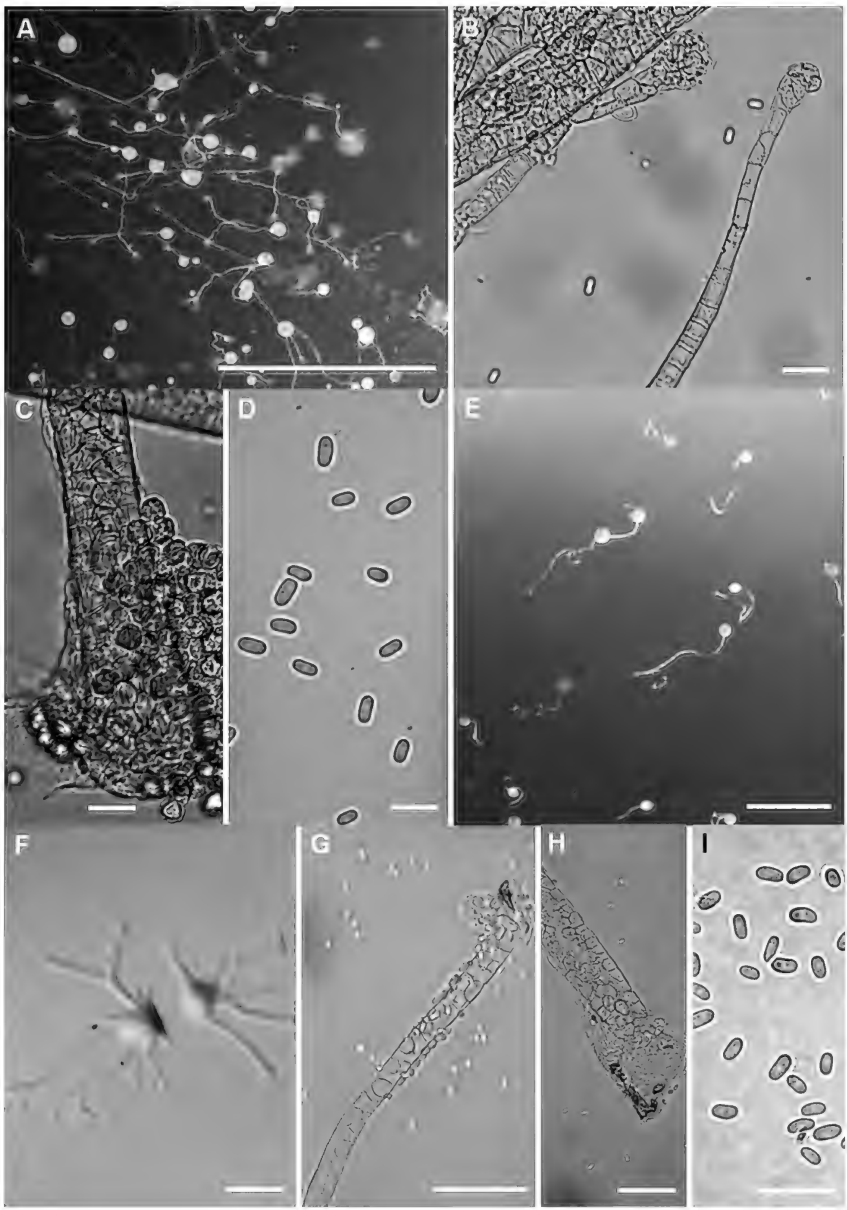

Plate 1. ***Dictyostelium quercibrachium*** (HMJAU MR238): A. Sorocarps; B. Sorophore tips; C. Sorophore base; D. Spores. ***Dictyostelium crassicaule*** (HMJAU MR230): E. Sorocarps; F. Aggregations, G. Sorophore tip; H. Sorophore base; I. Spores. Scale bars: A = 5 mm; B, C, I = 20 μm; D = 10 μm; E = 1 mm; F = 200 μm; G, H = 50 μm.

Specimen examined: **CHINA, Jilin Province**, Changbai Mountain, isolated from a soil sample (S4377) collected in a *Pinus koraiensis* Sieb. & Zucc. forest, 22 Aug. 2014 (HMJAU MR238).

Comments: *Dictyostelium quercibrachium* was first reported from forest soil sampled in New Zealand; however, other identical isolates also have been recovered from a bog environment in north central Ohio in the United States and from Iguazú in South America, as per unpublished data (Cavender & al. 2002). The sorocarp morphology varies considerably in *D. quercibrachium* depending upon environmental conditions such as temperature and food supply.

Dictyostelium crassicaule H. Hagiw.,
Bull. Natl. Sci. Mus., Tokyo, B 10: 67. 1984. Plate 1E–I

When cultured at 23 °C on non-nutrient agar with *E. coli*, sorocarps solitary, unbranched, rarely prostrate, 0.3–2.3 mm long. Sorophore colorless, sinuous, stout, tapering from bases to tips, consisting of one to two tiers of cells near the tip, bases round or conical sometimes with basal discs, tips capitate. Sori white, globose, commonly 40–230 μm diam. Spores hyaline, oblong to elliptical, 5.7–7.0 × 3.4–3.9 μm, usually without (but sometimes with) irregular polar granules. Aggregations with radiate streams.

Specimen examined: **CHINA, Jilin Province**, Changbai Mountain, isolated from a soil sample (S4372) collected in an alpine birch forest, 22 Aug. 2014 (HMJAU MR230).

Comments: *Dictyostelium crassicaule* was originally isolated from soil sampled in *Pinus pumila* of Chokai Mountain, Akita, Japan (Hagiwara 1984). This species is characterized by its small sorocarps, capitate tips, and thick sorophores.

Discussion

Our study increases to 20 the number of dictyostelid species known from Jilin Province. *Dictyostelium quercibrachium,* which was first reported from New Zealand in the Southern Hemisphere (Cavender & al. 2002), is new to China (here reported from a *Pinus koraiensis* forest) and is currently recorded only from Jilin and Heilongjiang provinces in China. Further dictyostelid surveys will probably increase species richness in Jilin Province.

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New host and distributional records for *Camarosporidiella* in Italy, Russia, and Ukraine

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Abstract—*Camarosporidiella* specimens collected from woody plants in central Italy, eastern Ukraine, and southeastern Russia were identified based on morphology and multi-gene (LSU, SSU, ITS, and TEF) sequence analyses. *Camarosporidiella caraganicola* on *Amorpha fruticosa*, *C. celtidis* on *Ulmus pumila*, *C. elaeagnicola* on *Cytisus ruthenicus* are described with new host records and as new fungal records for Ukraine. *Camarosporidiella moricola* on *Morus nigra* is newly reported for Italy, and *C. robiniicola* on *Robinia pseudoacacia* is new for Ukraine. *Camarosporidiella elaeagnicola* on *Elaeagnus angustifolia* is re-described to facilitate identification. Notes on host distribution of *Camarosporidiellaceae* are also provided.

Key words—asexual, multigene, phylogeny, taxa, taxonomy

Introduction

The monotypic family *Camarosporidiellaceae* was introduced by Wanasinghe & al. (2017) for *Camarosporidiella* as type genus. *Camarosporidiella* species, which are necrotrophic or saprobic on host plants (Tibpromma & al. 2017, Wanasinghe & al. 2017), are mainly distributed in southern (Italy) and eastern Europe (Russia), central Asia (Uzbekistan), and Southeast Asia (Thailand) (Wanasinghe & al. 2017). There are 23 *Camarosporidiella* records listed in Index Fungorum (2020, accessed 2 August). Understanding species relationships within *Camarosporidiella* is complicated due to the lack of morphological characters available to distinguish species. Most species are characterized by asexual morphs producing conidia that are muriform, ellipsoidal, or fusiform and dark brown (Wanasinghe & al. 2017). Species exhibiting a sexual morph are characterized by globose to subglobose ascomata, cylindrical short-pedicellate asci, and ellipsoidal muriform ascospores. Accurate new host-fungus records are essential for identification and prevention of plant diseases (Dugan & al. 2018). New fungal reports facilitate deposition of new voucher specimens, contribute new molecular data in GenBank, expand knowledge surrounding host-specificity, and note new host-fungi interactions (Halme & al. 2012). In this study, we describe and illustrate six *Camarosporidiella* species and analyze DNA sequences that may facilitate their species identification. *Camarosporidiella caraganicola*, *C. celtidis*, *C. elaeagnicola* have new host records for Ukraine, and *C. moricola* on *Morus nigra* (in Italy) and *C. robiniicola* (in Ukraine) represent new distributional records. *Camarosporidiella elaeagnicola* on *Elaeagnus angustifolia* is re-described to enable identification. Host distributions of all six species are also discussed.

Materials & methods

Sample collection, morphological examination, and isolation

Fresh specimens were collected from southern European Russia (Rostov region), eastern Ukraine (Donetsk region), and central Italy (Forlì-Cesena province). No endangered or protected species were sampled. Twigs, branches, and stems were examined for fruiting bodies in the laboratory using a Motic SMZ 168 stereomicroscope. Single spore cultures were established according to Chomnunti & al. (2014). Conidia and ascospores were lifted from fruiting bodies using a sterile inoculation needle and dropped onto surfaces of malt extract agar (MEA) plates that were kept in a dry place overnight. Plates were checked using the stereomicroscope, and single germinated conidia or ascospores were transferred to new MEA plates. The culture media were kept at 25°C for 10 days (Damm & al. 2009). MEA colony morphologies (including colour, shape, and growth rate) were determined after 7 days of incubation. Microscopic fungal structures were mounted in water and observed using a Nikon Eclipse 80i compound microscope and photographed with a Canon 750D digital camera fitted to the microscope.

Voucher specimens are deposited in the Herbarium of Mae Fah Luang University, Chiang Rai, Thailand (MFLU). Single-spore cultures were preserved on MEA in 1.5 mL microtube slants at 4°C in Mae Fah Luang Culture Collection, Chiang Rai, Thailand (MFLUCC) with duplicates at Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures, Braunschweig, Germany (DSM). Tarosoft (R) Image Frame Work was used to measure sizes of microstructure, and Adobe Photoshop CS6 Extended (v. 10.0) was used to prepare photographic plates.

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from scraped fresh fungal mycelium grown on MEA media for 8 weeks at 25°C by using the E.Z.N.A Fungal DNA Mini Kit (D3390-02) extraction kit following the manufacturer's protocol. Four regions [3′-end of 18S + ITS1+ 5.8S rRNA gene + ITS2 + 5′-end of the 28S rRNA gene; 28S rDNA gene (LSU); 18S rDNA gene (SSU); partial translation elongation factor 1-alpha gene (TEF)] were amplified and sequenced using the primer pairs ITS5 and ITS4 (White & al. 1990), LR0R (Rehner & Samuels 1994) and LR5 (Vilgalys & Hester 1990), NS1 and NS4 (White & al. 1990), and TEF1-983F and TEF1-2218R (Rehner & Buckley 2005). Polymerase chain reaction (PCR) mixtures and conditions for ITS, LSU, SSU, and TEF were amplified in 25-µL volumes according to Wanasinghe & al. (2017). Final mixtures comprised 1 µL genomic DNA extract, 12.5 µL of 2× Power Taq PCR MasterMix and 9.5 µL deionised water and 1 µL of each primer (10 µM). For each gene, PCR conditions included initial denaturation at 95°C for 5 min, 35 denaturation cycles at 95°C for 90 s, annealing for 90 s, elongation at 72°C for 1 min, and final extension at 72°C for 10 min. Annealing temperatures were 56°C for ITS and LSU, 55 °C for SSU, and 58°C for TEF. PCR amplicons were visualized under UV light on 1.2% agarose gels stained with GoldView (TM) Gel Stain. The PCR

Table 1. Details of *Camarosporidiella* species included in the phylogenetic study.

Species	Culture no[A]	Specimen no[B]	Host / substrate	Country	GenBank accession no.[C]			
					ITS	LSU	SSU	tef
C. aborescentis	CPC 31420	–	*Cytisus borysthenicus*	Ukraine	KY929127	KY929163	—	—
	MFLUCC 14-0604	–	*Colutea arborescens*	Russia	KP711377	KP711378	KP711379	—
	–	MFLU 15-2181	*Colutea orientalis*	Russia	MF434115	MF434202	MF434290	MF434378
	MFLUCC 17-0660	MFLU 15-3630	*Colutea arborescens*	Italy	MF434116	MF434203	MF434291	MF434379
	MFLUCC 17-0738	MFLU 16-2387	*Amorpha* sp.	Russia	MF434117	MF434204	MF434292	MF434380
C. arezzoensis	MFLUCC 14-0891	MFLU 17-0455	*Amorpha fruticosa*	Russia	MF434118	MF434205	MF434293	MF434381
	MFLUCC 14-0899 = CBS 143102	MFLU 17-0462	*Cytisus austriacus*	Russia	MF434119	MF434206	MF434294	MF434382
	MFLUCC 14-0913 = CBS 143103	MFLU 17-0475	*Cytisus borysthenicus*	Russia	MF434120	MF434207	MF434295	MF434383
	MFLUCC 14-0916 = CBS 143104	MFLU 17-0478	*Cytisus austriacus*	Russia	MF434121	MF434208	MF434296	MF434384
	MFLUCC 14-0238	MFLU14-0636	*Cytisus* sp.	Italy	—	KP120927	KP120928	—
C. caraganicola	MFLUCC 14–0605	MFLU 14–0794	*Caragana frutex*	Russia	KP711380	KP711381	KP711382	—
	MFLUCC 14-0887 = CBS 143105	MFLU 17-0453	*Caragana frutex*	Russia	MF434122	MF434209	MF434297	MF434385
	MFLUCC 14-0896 = CBS 143106	MFLU 17-0459	*Caragana frutex*	Russia	MF434123	MF434210	MF434298	MF434386
	MFLUCC 17-0697 = CBS 143107	MFLU 15-2242	*Caragana frutex*	Russia	MF434124	MF434211	MF434299	MF434387
	MFLUCC 17-0726 = CBS 143108	MFLU 16-1782	*Caragana frutex*	Russia	MF434125	MF434212	MF434300	MF434388
	MFLUCC 18-0786	**MFLU 17-2539**	***Amorpha fruticosa***	**Ukraine**	**MN244227**	**MN244210**	**—**	**MN587129**
C. celtidis	–	MFLU 15-3551	Unidentified stem	Italy	—	MF434213	MF434301	—
	MFLUCC 15-0444		*Celtis occidentalis*	Russia	KU697613	KU697614	KU697615	KU697612
	–	MFLU 15-1897	*Spiraea* sp.	Russia	MF434126	MF434214	MF434302	MF434389
	–	MFLU 15-2036	*Elymus repens*	Russia	MF434127	MF434215	MF434303	MF434390
	MFLUCC 14-0884 = CBS 143109	MFLU 17-0450	*Maclura pomifera*	Russia	MF434128	MF434216	MF434304	MF434391
	MFLUCC 14-0904 = CBS 143110	MFLU 17-0466	*Gleditsia triacanthos*	Russia	MF434129	MF434217	MF434305	MF434392

Species	Culture no[A]	Specimen no[B]	Host / substrate	Country	GenBank accession no.[C]			
					ITS	LSU	SSU	tef
	MFLUCC 17-0556	MFLU 15-2062	*Betula pendula*	Russia	MF434130	MF434218	MF434306	MF434393
	MFLUCC 17-0676 = CBS 143111	MFLU 15-1928	*Prunus padus*	Russia	MF434131	MF434219	MF434307	MF434394
	MFLUCC 17-0679	MFLU 15-1943	*Morus alba*	Russia	MF434132	MF434220	MF434308	MF434395
	MFLUCC 17-0701 = CBS 143112	MFLU 15-2912	*Ailanthus altissima*	Russia	MF434133	MF434221	MF434309	MF434396
	MFLUCC 17-0735	MFLU 16-2358	*Robinia* sp.	Russia	MF434134	MF434222	MF434310	MF434397
	MFLUCC 18-1134	**MFLU 17-2492**	***Ulmus pumila***	**Ukraine**	**MN244225**	**MN244208**	**MN244185**	—
C. clematidis	MFLUCC 13-0336	MFLU13–0336	*Clematis vitalba*	Italy	KJ562213	KJ562188	KJ589414	—
C. elaeagnicola	–	MFLU 15-1924	*Artemisia santonicum*	Russia	MF434135	MF434223	MF434311	MF434398
	–	MFLU 15-2215	*Elaeagnus angustifolia*	Russia	MF434136	MF434224	MF434312	MF434399
	MFLUCC 14-0908 = CBS 143113	MFLU 17-0470	*Elaeagnus angustifolia*	Russia	MF434137	MF434225	MF434313	MF434400
	MFLUCC 14-0911 = CBS 143114	MFLU 17-0473	*Elaeagnus angustifolia*	Russia	MF434138	MF434226	MF434314	MF434401
	MFLUCC 14-0912 = CBS 143115	MFLU 17-0474	*Elaeagnus angustifolia*	Russia	MF434139	MF434227	MF434315	MF434402
	MFLUCC 17-0705	MFLU 15-2956	*Elaeagnus angustifolia*	Russia	MF434140	MF434228	MF434316	MF434403
	MFLUCC 17-0706	MFLU 15-2958	*Elaeagnus angustifolia*	Russia	MF434141	MF434229	MF434317	MF434404
	MFLUCC 17-0707	MFLU 15-2962	*Elaeagnus angustifolia*	Russia	MF434142	MF434230	MF434318	MF434405
	MFLUCC 17-0712	MFLU 16-1481	*Elaeagnus angustifolia*	Russia	MF434143	MF434231	MF434319	MF434406
	MFLUCC 17-0737	MFLU 16-2382	*Elaeagnus angustifolia*	Russia	MF434144	MF434232	MF434320	MF434407
	CPC 31031		*Elaeagnus rhamnoides*	Germany	KY929131	KY929166	—	—
	MFLUCC 18-0782	**MFLU 17-2505**	*Cytisus ruthenicus*	**Ukraine**	**MN244226**	**MN244209**	**MN244186**	—
	MFLUCC 18-0788	**MFLU 17-2551**	***Elaeagnus angustifolia***	**Ukraine**	**MN244228**	**MN244211**	**MN244187**	**MN587132**
	MFLUCC 18-0764	**MFLU 17-1849**	***Elaeagnus angustifolia***	**Russia**	—	**MN244212**	**MN244188**	**MN587133**
C. elongata	CBS 171.55	–	*Robinia pseudoacacia*	Germany	—	DQ678061	DQ678009	DQ677904
	MFLUCC 14-0260	–	*Cytisus scoparius*	Germany	—	KJ724249	—	—
C. eufemiana	MFLUCC 17-0207 = CBS 143116	MFLU 16-0182	*Cytisus* sp.	Italy	MF434145	MF434233	MF434321	MF434408
C. halimodendri	MFLUCC 14-0901 = CBS 143117	MFLU 17-0463	*Caragana halodendron*	Russia	MF434146	MF434234	MF434322	MF434409

Species	Culture no[A]	Specimen no[B]	Host / substrate	Country	GenBank accession no.[C]			
					ITS	LSU	SSU	tef
	MFLUCC 14-0905	MFLU 17-0467	*Caragana halodendron*	Russia	MF434147	MF434235	MF434323	MF434410
	MFLUCC 14-0907 = CBS 143118	MFLU 17-0469	*Caragana frutex*	Russia	MF434148	MF434236	MF434324	MF434411
	MFLUCC 14-0914	MFLU 17-0476	*Cytisus podolicus*	Russia	MF434149	MF434237	MF434325	MF434412
	MFLUCC 17-0212 = CBS 143119	MFLU 15-2123	*Lycium barbarum*	Russia	MF434150	MF434238	MF434326	MF434413
	MFLUCC 17-0691	MFLU 15-2172	*Caragana halodendron*	Russia	MF434151	MF434239	MF434327	MF434414
	MFLUCC 18-0767	**MFLU 17-2008**	***Robinia pseudoacacia***	**Russia**	**MN244235**	**MN244219**	**MN244195**	—
C. italica	MFLUCC 13-0547	MFLU 17-0139	*Hippocrepis emerus*	Italy	MF434152	MF434240	MF434328	MF434415
C. laburni	MFLUCC 14-0885	MFLU 17-0451	*Laburnum anagyroides*	Russia	MF434153	MF434241	MF434329	MF434416
	MFLUCC 14-0919 = CBS 143121	MFLU 16-0094	*Laburnum anagyroides*	Italy	MF434154	MF434242	MF434330	MF434417
	MFLUCC 17-0704 = CBS 143122	MFLU 15-2954	*Laburnum anagyroides*	Russia	MF434155	MF434243	MF434331	MF434418
	MFLUCC 17-0709	MFLU 15-2981	*Laburnum* sp.	Russia	MF434156	MF434244	MF434332	MF434419
	MFLUCC 17-0751 = CBS 143120	MFLU 17-1434	*Laburnum anagyroides*	Russia	MF434157	MF434245	MF434333	MF434420
	MFLUCC 17-0752	MFLU 17-1435	*Laburnum anagyroides*	Russia	MF434158	MF434246	MF434334	MF434421
C. laburnicola	MFLUCC 14-0565	MFLU 15-1522	*Laburnum anagyroides*	Russia	:KY497784	KY497779	KY497781	KY497785
C. mackenziei	MFLUCC 14-0883 = CBS 143123	MFLU 17-0449	*Caragana arborescens*	Russia	MF434159	MF434247	MF434335	MF434422
	MFLUCC 14-0893 = CBS 143124	MFLU 17-0457	*Caragana arborescens*	Russia	MF434160	MF434248	MF434336	MF434423
	MFLUCC 17-0703	MFLU 15-2953	*Caragana* sp.	Russia	MF434161	MF434249	MF434337	MF434424
	CPC 25960		*Caragana* sp.	Finland	KY929129	KY929164	—	KY929198
	CPC 25962		*Caragana* sp.	Finland	KY929130	KY929165		KY929199
C. melnikii	MFLUCC 17-0684	MFLU 15-2022	*Caragana frutex*	Russia	MF434162	MF434250	MF434338	MF434425
C. mirabellensis	–	MFLU 17-228	*Robinia pseudoacacia*	Russia	MF434163	MF434251	MF434339	MF434426
C. mori		MFLU 17-2147	*Morus alba*	Russia	MK590359	MK590358	—	—
C. moricola	–	MFLU 15-1936	*Morus alba*	Russia	MF434164	MF434252	MF434340	MF434427
	–	MFLU 15-2223	*Morus alba*	Russia	MF434165	MF434253	MF434341	MF434428
	MFLUCC 14-0886	MFLU 17-0452	*Morus alba*	Russia	MF434166	MF434254	MF434342	MF434429

Species	Culture no[A]	Specimen no[B]	Host / substrate	Country	GenBank accession no.[C]			
					ITS	LSU	SSU	tef
	MFLUCC 14-0898	MFLU 17-0461	*Morus alba*	Russia	MF434167	MF434255	MF434343	MF434430
	MFLUCC 16-1396	MFLU 15-2075	*Morus alba*	Russia	KY053887	KY053890	KY053893	—
	MFLUCC 16-1397	MFLU 15-2222	*Morus alba*	Russia	KY053888	KY053891	KY053894	—
	MFLUCC 16-1398	MFLU 15-2223	*Morus alba*	Russia	KY053889	KY053892	KY053895	—
	MFLUCC 17-0680	MFLU 15-1969	*Morus alba*	Russia	MF434168	MF434256	MF434344	MF434431
	MFLUCC 17-0687	MFLU 15-2075	*Morus alba*	Russia	MF434169	MF434257	MF434345	MF434432
	MFLUCC 17-0694	MFLU 15-2222	*Morus alba*	Russia	MF434170	MF434258	MF434346	MF434433
	MFLUCC 17-0711	MFLU 15-2999	*Morus alba*	Russia	MF434171	MF434259	MF434347	MF434434
	MFLUCC 17-0714 = CBS 143125	MFLU 16-1527	*Morus alba*	Russia	MF434172	MF434260	MF434348	MF434435
	MFLUCC 17-0718 = CBS 143126	MFLU 16-1626	*Morus alba*	Russia	MF434173	MF434261	MF434349	MF434436
	MFLUCC 17-0719	MFLU 16-1639	*Morus alba*	Russia	MF434174	MF434262	MF434350	MF434437
	MFLUCC 17-0725	MFLU 16-1770	*Morus alba*	Russia	MF434175	MF434263	MF434351	MF434438
	MFLUCC 18-0766	**MFLU 17-1904**	***Morus alba***	**Russia**	**MN244229**	**MN244213**	**MN244189**	—
	MFLUCC 18-0768	**MFLU 17-2010**	***Morus alba***	**Russia**	**MN244230**	**MN244214**	**MN244190**	MN587134
	MFLUCC 18-0769	**MFLU 17-2035**	***Morus alba***	**Russia**	**MN244231**	**MN244215**	**MN244191**	MN587135
	MFLUCC 18-0770	**MFLU 17-2036**	***Morus alba***	**Russia**	**MN244232**	**MN244216**	**MN244192**	MN587136
	MFLUCC 18-0771	**MFLU 17-2060**	***Morus alba***	**Russia**	**MN244233**	**MN244217**	**MN244193**	**MN587137**
	MFLUCC 18-0772	**MFLU 17-2085**	***Morus alba***	**Russia**	**MN244234**	**MN244218**	**MN244194**	—
	MFLUCC 17-2310	**MFLU 17-0991**	***Morus nigra***	**Italy**	**MN603933**	**MN608782**	—	**MN587138**
C. populina	MFLUCC 18-0087	MFLU 16-1722	*Populus nigra*	Russia	NR_161040	—	NG_065721	—
C. premilcurensis	MFLUCC 17-0208 = CBS 143127	MFLU 16-0185	*Cytisus* sp.	Italy	MF434176	MF434264	MF434352	MF434439
C. robiniicola	MFLUCC 13-0527	MFLU 13-0340	*Robinia pseudoacacia*	Italy	KJ562214	KJ589412	KJ589415	—
	MFLUCC 14-0892 = CBS 143128	MFLU 17-0456	*Gleditsia triacanthos*	Russia	MF434177	MF434265	MF434353	MF434440
	MFLUCC 14-0894 = CBS 143129	MFLU 17-0458	*Robinia neomexicana*	Russia	MF434178	MF434266	MF434354	MF434441
	MFLUCC 14-0906 = CBS 143130	MFLU 17-0468	*Gleditsia triacanthos*	Russia	MF434179	MF434267	MF434355	MF434442

Species	Culture no[a]	Specimen no[b]	Host / substrate	Country	GenBank accession no.[c]			
					ITS	LSU	SSU	TEF
	MFLUCC 14-0909 = CBS 143131	MFLU 17-0471	*Robinia pseudoacacia*	Russia	MF434180	MF434268	MF434356	MF434443
	MFLUCC 17-0688	MFLU 15-2104	*Robinia pseudoacacia*	Russia	MF434181	MF434269	MF434357	MF434444
	MFLUCC 17-0716 = CBS 143132	MFLU 16-1597	*Robinia* sp.	Russia	MF434182	MF434270	MF434358	MF434445
	MFLUCC 17-0733	MFLU 16-2300	*Robinia* sp.	Russia	MF434183	MF434271	MF434359	MF434446
	CPC 27667	–	*Robinia pseudoacacia*	Ukraine	KY929133	KY929168	—	—
	CPC 30379	–	*Philadelphus coronarius*	Germany	KY929134	KY929169	—	—
	MFLUCC 18-0775	**MFLU 17-2469**	***Robinia pseudoacacia***	**Ukraine**	**MN244236**	**MN244220**	**MN244196**	**MN587130**
	MFLUCC 18-0789	**MFLU 18-0320**	***Robinia pseudoacacia***	**Russia**	**MN244224**	**MN244207**	**MN244184**	**MN587131**
	MFLUCC 14-0620	MFLU 14-0770	*Cotinus coggygria*	Russia	KP744436	KP744478	KP753948	
C. schulzeri	–	MFLU 15-1909	*Gleditsia triacanthos*	Russia	MF434184	MF434272	MF434360	MF434447
	MFLUCC 14-0897 = CBS 143133	MFLU 17-0460	*Elaeagnus angustifolia*	Russia	MF434185	MF434273	MF434361	MF434448
	MFLUCC 17-0717	MFLU 16-1599	*Robinia* sp.	Russia	MF434186	MF434274	MF434362	MF434449
	MFLUCC 17-0722	MFLU 16-1664	*Robinia* sp.	Russia	MF434187	MF434275	MF434363	MF434450
Camarosporidiella sp.	CPC 31632	–	*Ulmus laevis*	Ukraine	KY929132	KY929132	—	—
Camarosporidiella sp.	CPC 12441	–	*Sophora chrysophylla*	Hawaii	KY929128	DQ377885	—	—
C. spartii	MFLUCC 14-0915	MFLU 17-0477	*Cytisus ruthenicus*	Russia	MF434188	MF434276	MF434364	MF434451
	MFLUCC 17-0713 = CBS 143134	MFLU 16-1484	*Bassia* sp.	Russia	MF434189	MF434277	MF434365	MF434452
	MFLUCC 13-0548	–	*Cytisus* sp.	Italy	KJ562215	—	—	—

[a] Culture Collection of the Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; MFLUCC: Mae Fah Luang University

[b] Culture Collection, Chiang Rai, Thailand. MFLU: Mae Fah Luang University (MFLU) Herbarium, Chiang Rai, Thailand; TASM: Tashkent Mycological Herbarium, Institute of Botany and Zoology, Academy of Sciences of Uzbekistan, Tashkent, Uzbekistan.

[c] ITS: Internal transcribed spacers; LSU: partial 28S nrDNA; SSU: partial 18S nrDNA; TEF: translation elongation factor 1-alpha gene.

Newly generated sequences are shown in bold.

amplification products (amplimers) were analysed by the BGI, Ltd (Shenzhen, PR China). Same primer pairs used for amplification process were used for sequencing. The nucleotide sequences were deposited in GenBank (Table 1), and the final alignment and tree are deposited in TreeBASE (http://www.treebase.org/).

Phylogenetic and sequence analysis

The raw trace files were edited using BioEdit v. 7.0.5.2 (Hall 1999) and unclear peaks were omitted from the beginning and end of the sequences. A consensus sequence was generated manually for each set of trace files from the forward and reverse sequences, which were subjected to standard GenBank BLAST searches to compare with other fungal DNA sequences from NCBIs GenBank sequence database. High similarity sequences were added to the alignments. Sequences generated in this study and those obtained from GenBank were aligned using MAFFT (Kuraku & al. 2013, Katoh & al. 2017) and adjusted visually in BioEdit v. 7.0.5.2. The best evolutionary model for each data partition was obtained using MrModelTest v. 2.3 (Nylander 2004) under the Akaike Information Criterion (AIC) implemented in both PAUP v. 4.0b10 and MrBayes v. 3. The combined gene trees were phylogenetically regenerated using both Bayesian Inference (BI) and Maximum Likelihood (ML) criteria as outlined in Jeewon & al. (2017), Pem & al. (2019a,b), and Senanayake & al. (2017). ML analysis was conducted in RAxML-HPC2 on XSEDE (8.2.8) (Stamatakis 2006) implemented in raxmlGUI v.0.9b2 (Silvestro & Michalak 2012), employing GTR+I+G evolutionary settings; bootstrap support values were obtained by running 1000 pseudo replicates. Bayesian inference (BI) analysis was run with MrBayes v. 3.2.1 (Ronquist & Huelsenbeck 2003) to evaluate Posterior probabilities (BYPP) (Rannala & Yang 1996, Zhaxybayeva & Gogarten 2002) with Markov Chain Monte Carlo (MCMC) sampling. The heating parameter was set at 0.15. Two parallel runs were conducted using the default settings. The analysis lasted until the average standard deviation of split frequencies came below 0.01. Trees were saved each 1000 generation, with the first 25% discarded as the 'burn-in' phase. BYPP were calculated from the remaining trees. The resulting phylogenetic tree was visualized with FigTree v1.4.0 program (Rambaut 2012) and reorganized in Microsoft Power Point 2007 and Adobe Illustrator CS5 (v. 15.0.0). Sequences generated in this study were submitted to NCBI's GenBank nucleotide database (http://www.ncbi.nlm.nih.gov; Table 1).

Phylogenetic results

Topologies of ML and BI trees recovered for each gene dataset were visually compared, and the overall tree topology was congruent to those obtained from the combined dataset. The RAxML analysis of the combined dataset yielded a best scoring tree (Fig. 1a,b,c) with a final ML optimization likelihood value of –7746.830774. The matrix had 412 distinct alignment patterns, with 11.62% proportion of gaps and completely undetermined characters in this alignment. Parameters for the GTR + I + G model of

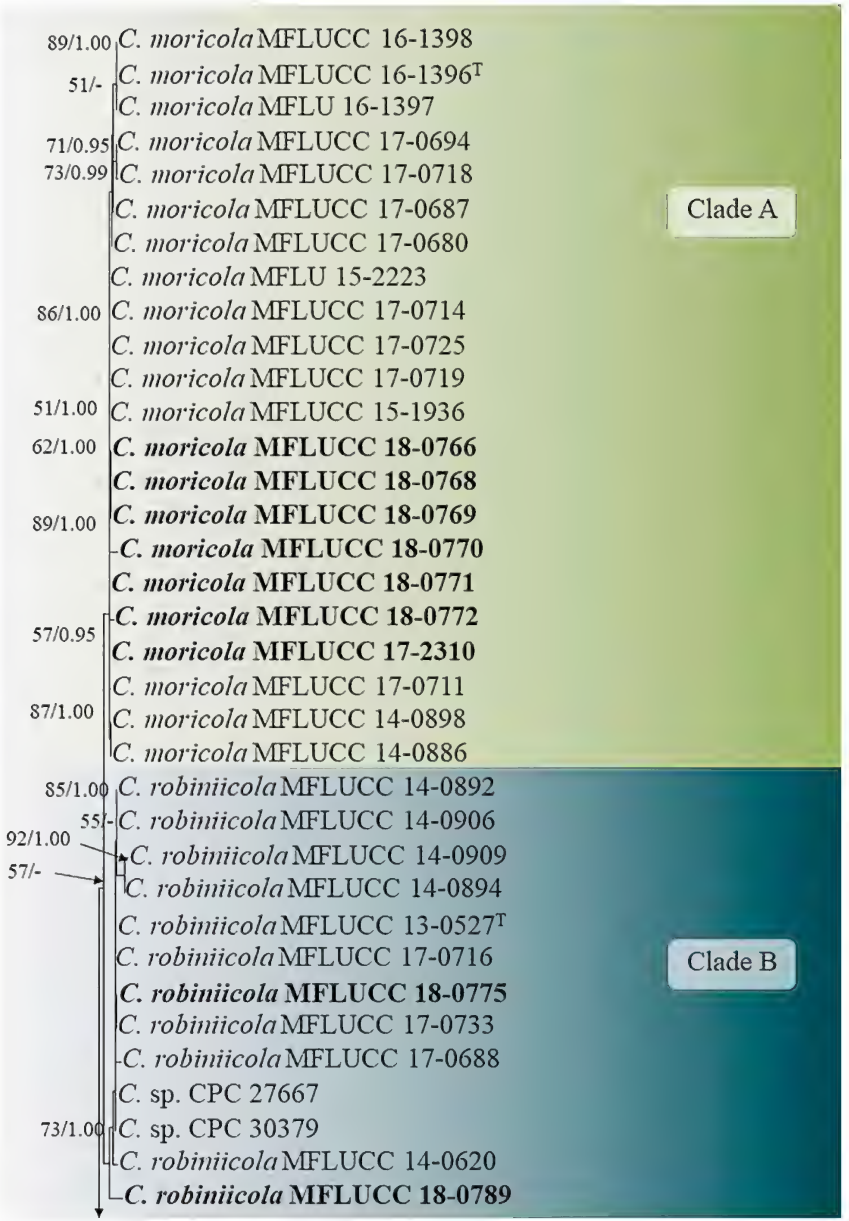
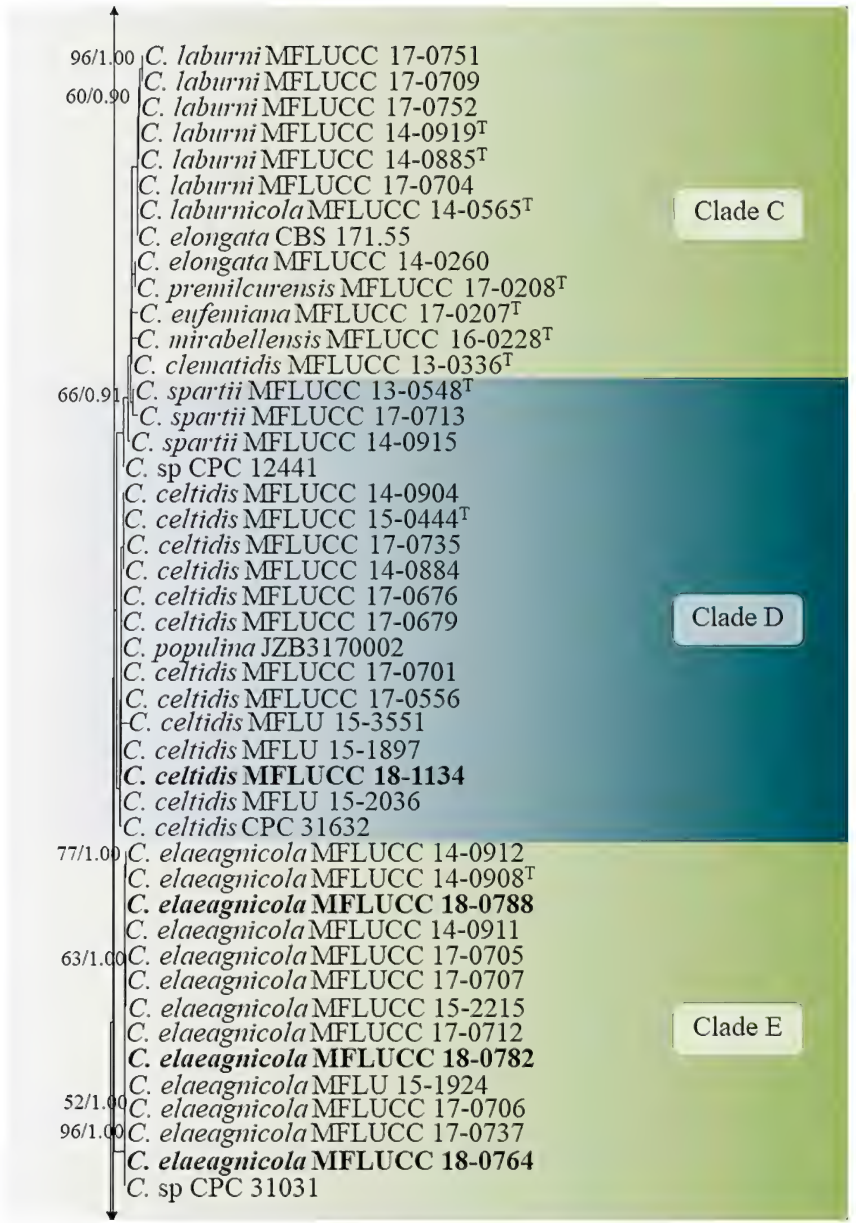
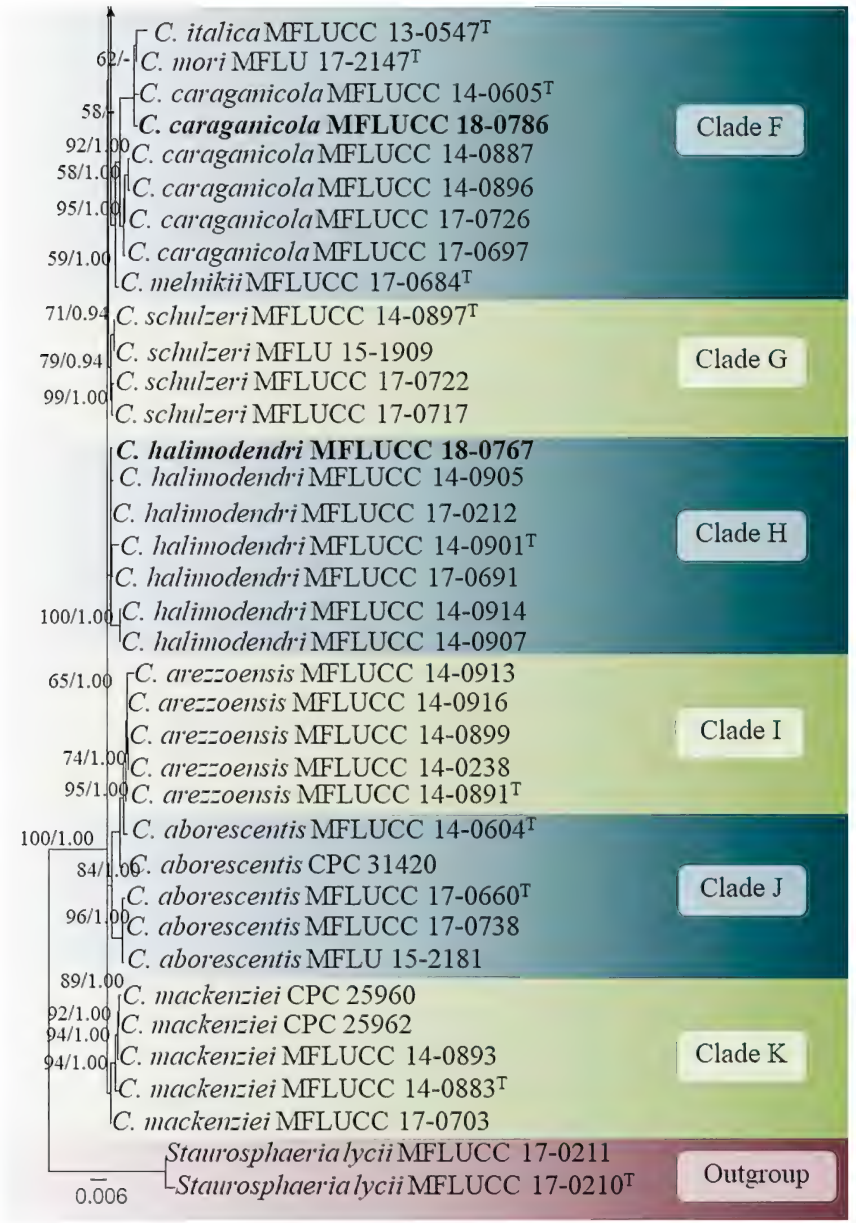


FIG. 1a–c (pp.460–462). RAxML tree of *Camarosporidiella* spp. based on analysis of a combined dataset of LSU, SSU, ITS, and TEF partial sequence data. Bootstrap support values for ML ≥50% and Bayesian posterior probabilities (PP) ≥0.90 are presented as ML/PP above and below the



nodes. The new isolates are set in bold font. Ex-type strains are indicated with a superscript [T]. The scale bar represents the expected number of nucleotide substitutions per site.


C. italica MFLUCC 13-0547T
C. mori MFLU 17-2147T
C. caraganicola MFLUCC 14-0605T
C. caraganicola MFLUCC 18-0786
C. caraganicola MFLUCC 14-0887
C. caraganicola MFLUCC 14-0896
C. caraganicola MFLUCC 17-0726
C. caraganicola MFLUCC 17-0697
C. melnikii MFLUCC 17-0684T
C. schulzeri MFLUCC 14-0897T
C. schulzeri MFLU 15-1909
C. schulzeri MFLUCC 17-0722
C. schulzeri MFLUCC 17-0717
C. halimodendri MFLUCC 18-0767
C. halimodendri MFLUCC 14-0905
C. halimodendri MFLUCC 17-0212
C. halimodendri MFLUCC 14-0901T
C. halimodendri MFLUCC 17-0691
C. halimodendri MFLUCC 14-0914
C. halimodendri MFLUCC 14-0907
C. arezzoensis MFLUCC 14-0913
C. arezzoensis MFLUCC 14-0916
C. arezzoensis MFLUCC 14-0899
C. arezzoensis MFLUCC 14-0238
C. arezzoensis MFLUCC 14-0891T
C. aborescentis MFLUCC 14-0604T
C. aborescentis CPC 31420
C. aborescentis MFLUCC 17-0660T
C. aborescentis MFLUCC 17-0738
C. aborescentis MFLU 15-2181
C. mackenziei CPC 25960
C. mackenziei CPC 25962
C. mackenziei MFLUCC 14-0893
C. mackenziei MFLUCC 14-0883T
C. mackenziei MFLUCC 17-0703
Staurosphaeria lycii MFLUCC 17-0211
Staurosphaeria lycii MFLUCC 17-0210T
62/-
58/-
92/1.00
58/1.00
95/1.00
59/1.00
71/0.94
79/0.94
99/1.00
100/1.00
65/1.00
74/1.00
95/1.00
100/1.00
84/1.00
96/1.00
89/1.00
92/1.00
94/1.00
94/1.00
0.006
Clade F
Clade G
Clade H
Clade I
Clade J
Clade K
Outgroup

the combined LSU, ITS, SSU and TEF were as follows: Estimated base frequencies: A = 0.243219, C = 0.241435, G = 0.266791, T = 0.248554; substitution rates AC = 1.018686, AG = 2.994042, AT = 1.771673, CG = 1.029209, CT = 4.405919, GT = 1.000000; proportion of invariable sites I = 0.845457; gamma distribution shape parameter α = 0.909328. The Bayesian analysis resulted in 10,000 trees after 1 M generations with 0.049881 as the average standard deviation of split frequency. The first 2000 trees representing the burn-in phase of the analyses were discarded, and the remaining 8000 trees were used for calculating posterior probabilities in the majority rule consensus tree.

Newly generated sequences from seven *Camarosporidiella* isolates (MFLUCC 18-0766, MFLUCC 18-0768, MFLUCC 18-0769, MFLUCC 18-0770, MFLUCC 18-0771, MFLUCC 18-0772, and MFLUCC 17-2310) grouped with isolates previously circumscribed as *C. moricola* (Wanasinghe & al. 2017, Tibpromma & al. 2017). These sequences formed a distinct clade (Fig. 1, Clade A) within *Camarosporidiella*, but were poorly supported in multi-gene analyses (MI = 62%, BI = 1; and ML = 89%, BI = 1). Two other isolates (MFLUCC 18-0775 and MFLUCC 18-0789) showed a close phylogenetic affinity with *C. robiniicola* strains and two unidentified *Camarosporidiella* species (CPC 27667 and CPC 30379); this relationship retrieved a support of ML = 73%, BI = 1 (Fig. 1, Clade B). Isolate MFLUCC 18-1134 clustered with *C. celtidis* strains (Fig. 1, Clade D). Three newly generated sequences, MFLUCC 18-0764, MFLUCC 18-0782, and MFLUCC 18-0788 grouped with *C. elaeagnicola* isolates with statistical support (ML = 60%, BI = 1). (Fig. 1, Clade E). Isolate MFLUCC 18-0786 clustered with *C. caraganicola* (MFLUCC 14-0605), *C. mori* (MFLU 17-2147), and *C. italica* (MFLUCC 13-0547) (Fig. 1, Clade F). MFLUCC 18-0767 nested among *C. halimodendri* isolates including ex-type strain (MFLUCC 14-0901) (Fig. 1, Clade H).

Taxonomy

Camarosporidiella caraganicola (Phukhams., Bulgakov & K.D. Hyde) Phukhams., Wanas. & K.D. Hyde, Stud. Mycol. 87: 220 (2017)

Plate 1, Fig. 2e,f

Saprobic on dead branches of *Amorpha fruticosa* L. (*Fabaceae*). Sexual morph: Ascomata 200–380 µm high, 250–380 µm diam. (x = 333.4 × 286.1 µm, n = 10), black, superficial to semi-immersed, in groups, occasionally dispersed underneath the host periderm, entirely or moderately erumpent,

Plate. 1. *Camarosporidiella caraganicola* (MFLU 17-2539). a, b. Ascomata on host surface; c. Ascoma, vertical section; d, e. Peridium; f. Hamathecium; g–j. Asci; k–r. Ascospores. Scale bars: a = 1000 µm; b = 500 µm; c = 200 µm; d, e = 25 µm; f = 5 µm; g–j = 50 µm; k–r = 10 µm.

globose, rough, ostiolate. Ostiole central, short, slightly sunken, tiny, inconspicuous on surface, smooth, with ostiolar canal filled with hyaline cells. Peridium 80–90 µm at the base, 60–90 µm on the sides, comprising 3–4 layers, with outer layer cells heavily pigmented, thick-walled, dark brown

cells of a textura angularis and the cells towards the inside lightly coloured with an inner layer comprising 3–4 layers, hyaline, flattened, thin-walled, a textura angularis. Hamathecium comprising numerous pseudoparaphyses 2.8–3.6 µm (n = 20) diam., filamentous, branched, septate. Asci 150–180 × 10–12 µm (x = 163.8 × 11.7 µm, n = 30), 8-spored, bitunicate, fissitunicate, cylindrical, short-pedicellate, rounded at apex with a tiny ocular chamber. Ascospores 20–24 × 7–8 µm (x = 22.9 × 7.3 µm, n = 50), overlapping uniseriate, muriform, ellipsoidal, 3–5-transversely septate, with 2–4 vertical septa, constricted at middle septum, initially hyaline and becoming brown at maturity, marginally paler, pointed and narrow at the ends, not surrounded by a mucilaginous sheath.

Culture Characteristics: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with dense mycelium, circular, rough margin, hairy, white at first, greenish grey after 2 months, reverse greenish grey in the middle, whitish at the margin, flat on the surface.

Specimen examined: **UKRAINE, Donetsk Region, Donetsk city,** Donetsk Botanical Garden, lower park near pond, dying and dead twigs of *Amorpha fruticosa*, 20 May 2017, Timur S. Bulgakov (MFLU 17-2539; living cultures MFLUCC 18-0786, DSM 109978).

Notes: Our specimen of *Camarosporidiella caraganicola* is morphologically and phylogenetically similar to another specimen collected from a different host, *Caragana frutex* (L.) K. Koch (*Fabaceae*); we isolated our strain from *Amorpha fruticosa*. Liu & al. (2015) reported the asexual morph, and Wanasinghe & al. (2017) reported the sexual morph. The phylogenetic placement of our strain (MFLUCC 18-1128) is shown in Fig. 1.

Hosts: *Caragana frutex* (Liu & al. 2015, Wanasinghe & al. 2017); *Amorpha fruticosa* (this study).

Distribution: Russia: Liu & al. 2015, Wanasinghe & al. 2017; Ukraine: this study).

Camarosporidiella celtidis (Shear) Thambug., Wanas. & K.D. Hyde, Stud. Mycol. 87: 226 (2017) Plate 2, Fig. 2c,d

Saprobic on dead twigs of *Ulmus pumila* L. (*Ulmaceae*).

Asexual morph: Conidiomata 250–350 µm high, 220–470 µm diam. (x = 280.5 × 314.7 µm, n = 10), solitary or gregarious, black, immersed to semi-immersed, unilocular, ostiolate. Conidiomatal wall 25–50 µm thick at the base, 25–35 µm and thick at the sides, comprising 3–4 layers, outer layer heavily pigmented, thick-walled, comprising dark reddish-brown cells of textura angularis, cells towards the inside lighter with the inner layer comprising 3–4 layers, hyaline, with thick-walled cells of textura

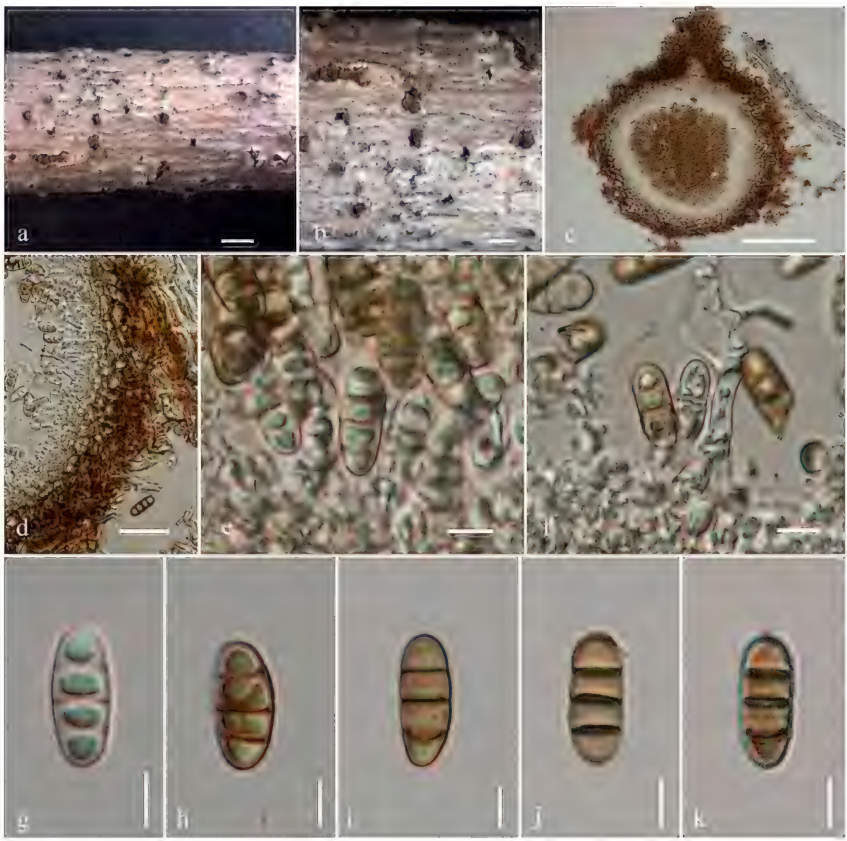


Plate. 2. *Camarosporidiella celtidis* (MFLU 17-2492). a, b. Conidiomata on host surface; c. Conidioma, vertical section; d. Peridium; e–f. Conidiogenous cells and developing conidia; g–k. Conidia. Scale bars: a, b = 500 µm; c = 100 µm; d = 30 µm; e–k = 5 µm.

angularis. Ostiole 25–30 µm long, 30–40 µm diam. (x = 26.5 × 37.5 µm, n = 6), central, smooth, ostiolar canal filled with hyaline or pale brown cells. Conidiophores reduced to conidiogenous cells. Conidiogenous cells enteroblastic, annellidic, doliiform, integrated, solitary, hyaline, smooth-walled, and formed from the inner layer of conidiomatal wall. Conidia 9–14 × 4–5 µm (x = 12.3 × 5.0 µm, n = 40), oblong, straight, rounded at both ends, 2–3-transversely euseptate, without vertical septa, smooth-walled, slightly constricted at septa, initially hyaline, becoming brown to dark brown at maturity.

Culture Characteristics: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with medium dense mycelium, circular smooth entire margin, radially furrowed, hairy, white at first, yellowish white after 2 months, reverse off white in the middle, white at the margin, flat on the surface.

Specimen examined: **UKRAINE, Donetsk region, Shakhtyoarsk district,** "Donetsk Ridge" regional landscape park ("Donetskiy kryazh"), old artificial forest belt, on *Ulmus pumila*, 19 May 2017, Timur S. Bulgakov (MFLU 17-2492; living cultures MFLUCC 18-1134, DSM 109786).

Notes: Our isolate MFLUCC 18-1134 clustered with the ex-type strain of *Camarosporidiella celtidis*, previously described by Wanasinghe & al. (2017). The main difference between descriptions by Wanasinghe & al. (2017) and our *C. celtidis* isolate is the size of conidia (15–20 × 6–8 µm vs. 9–14 × 4–5 µm). However, our LSU, SSU, ITS, and TEF sequence analyses showed a 100% similarity between our isolate and the other *C. celtidis* isolates in GenBank. In view of the phylogenetic and morphological similarities, we introduce our collection as a new record on *Ulmus pumila*.

Hosts: *Ailanthus altissima* (Mill.) Swingle, *Betula pendula* Roth, *Celtis occidentalis* L., *Elymus repens* (L.) Gould, *Gleditsia triacanthos* L., *Maclura pomifera* (Raf.) C.K. Schneid., *Morus alba* L., *Prunus padus* L., *Spiraea* sp., (Thambugala & al. 2016, Wanasinghe & al. 2017); *Ulmus pumila* (this study).

Distribution: Russia (Thambugala & al. 2016, Wanasinghe & al. 2017); Ukraine (this study).

Camarosporidiella elaeagnicola Wanas., Bulgakov & K.D. Hyde, Stud. Mycol. 87: 227 (2017) Plate 3, Fig. 2g,h

Necrotrophic on dying twigs.

Sexual morph: Undetermined.

Asexual morph: Conidiomata pycnidial, 170–270 µm high, 180–330 µm diam. (x = 259.4 × 204.6 µm, n = 10), solitary or gregarious, black, immersed to slightly erumpent, unilocular, ostiolate. Ostiole 17–20 µm long, 19–25 µm diam. (x = 15.2 × 19.1 µm, n = 10), central, smooth, ostiolar canal filled with hyaline or pale brown cells. Conidiomatal wall multi-layered, 25–35 µm thick at the base, 35–50 µm thick at the sides, comprising 5–8 layers of heavily pigmented dark brown cells of textura angularis, with lighter cells towards the inside, with inner layer comprising 2–4 layers, cells a textura angularis, hyaline, thin-walled. Macroconidiophores reduced to conidiogenous cells. Macroconidiogenous Cells enteroblastic with percurrent annellations, doliiform, integrated, solitary, hyaline, smooth-walled, and formed from the inner layer of conidiomatal wall.

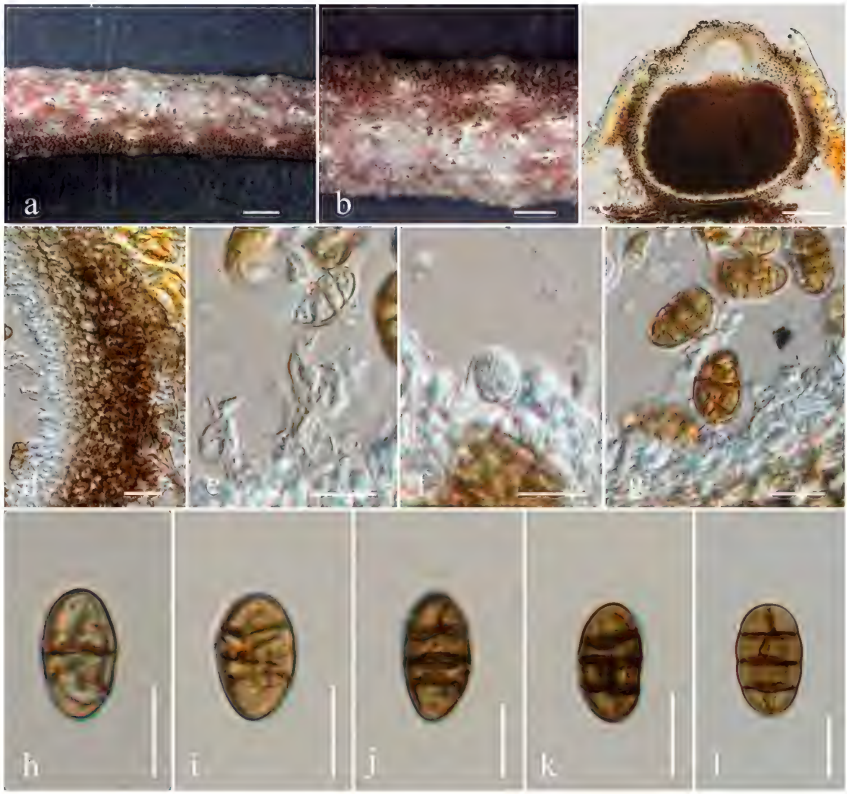


Plate. 3. *Camarosporidiella elaeagnicola* (MFLU 17-2505). a, b. Conidiomata on host surface; Conidioma, vertical section; d. Peridium; e–g. Conidiogenesis; h–l. Conidia. Scale bars: a = 1000 µm; b = 500 µm; c = 25 µm; d = 20 µm; e–l = 10 µm.

Macroconidia 13–18 × 8–9 µm (x = 15.5 × 9.0 µm, n = 30), ellipsoidal, straight to slightly curved, rounded at both ends, 2–3-transversely septate, with 2–4 vertical septa, muriform, smooth, pale to dark brown.

Culture Characteristics: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with dense mycelium, circular, smooth well-defined margin, hairy, white at the centre, greenish grey towards margin, reverse greenish grey, flat on the surface.

Specimens examined: **UKRAINE, Donetsk region, Shakhtyorsk district**, "Donetsk Ridge" regional landscape park ("Donetskiy kryazh"), stony steppe, on dying twigs of *Cytisus ruthenicus* Wol. [≡ *Chamaecytisus ruthenicus* (Wol.) Klásk.], 19 May

2017, Timur S. Bulgakov (MFLU 17-2505; living culture MFLUCC 18-0782, DSM 109783); **Donetsk city**, Donetsk Botanical Garden, arboretum park near the pond, on dead twigs of *Elaeagnus angustifolia*, 21 May 2017, Irina V. Bondarenko-Borisova (MFLU 17-2551; living culture MFLUCC 18-0788, DSM 109784); **RUSSIA**, **Rostov region**, **Shakhty city district**, rock quarry "Stony pond" ("Kamennyy stav"), on dead twigs of *Elaeagnus angustifolia*, 17 April 2017, Timur S. Bulgakov (MFLU 17-1849; living culture MFLUCC 18-0764; DSM 109794).

Notes: Our isolate MFLUCC 18-0782 clustered with the ex-type strains of *Camarosporidiella elaeagnicola* originally described by Wanasinghe & al. (2017). However, MFLUCC 18-0782 differs from the type strain in its comparatively smaller conidiomata (170–270 µm high, 185–330 µm diam. vs. 300–500 µm high, 300–550 µm diam.) and shorter conidia (13–18 × 8–9 µm vs. 18–25 × 9–13 µm). MFLUCC 18-0782 originates from Ukraine, while the holotype specimen was collected from an adjacent area of Russia. We provide identify this new collection as *C. elaeagnicola* based on its morphology, phylogeny, and host association.

Hosts: *Artemisia santonicum* (*Asteraceae*), *Cytisus ruthenicus* [≡ *Chamaecytisus ruthenicus*] (this study), *Elaeagnus angustifolia* (Wanasinghe & al. 2017).

Distribution: Russia (Wanasinghe & al. 2017), Ukraine (this study).

Camarosporidiella halimodendri Wanas., Bulgakov & K.D. Hyde, Stud. Mycol. 87: 230 (2017) Plate 4, Fig. 2a,b

Saprobic on dead branches of *Robinia pseudoacacia* L. (*Fabaceae*).

Sexual morph: Undetermined.

Asexual morph: Conidiomata pycnidial, 340–490 µm high, 440–710 µm diam. (x = 586.6 × 396.3 µm, n = 10), solitary or gregarious, black, immersed or semi-immersed, unilocular papillate. Ostiole 35–60 µm long, 40–60 µm diam. (x = 42.5 × 54.6 µm, n = 6), central, smooth, ostiolar canal filled with hyaline or pale brown cells. Conidiomatal wall comprising 1–2 layer of hyaline (inner layer) and dark reddish-brown (outer layer) cells of textura angularis. Conidiophores reduced to conidiogenous cells. Macroconidiogenous Cells enteroblastic, annellidic, doliiform, integrated, solitary, hyaline, smooth-walled, and formed from the inner layer of conidiomatal wall. Macroconidia 11–22 × 5–7 µm (x = 14.8 × 6.9 µm, n = 20), oblong, straight to slightly curved, rounded at both ends, 3–7-transversely septate, with 1–2 vertical septa, with 2–3 oblique septa, muriform, smooth-walled, hyaline when immature becoming dark brown on maturity. Microconidiogenous Cells intermixed with

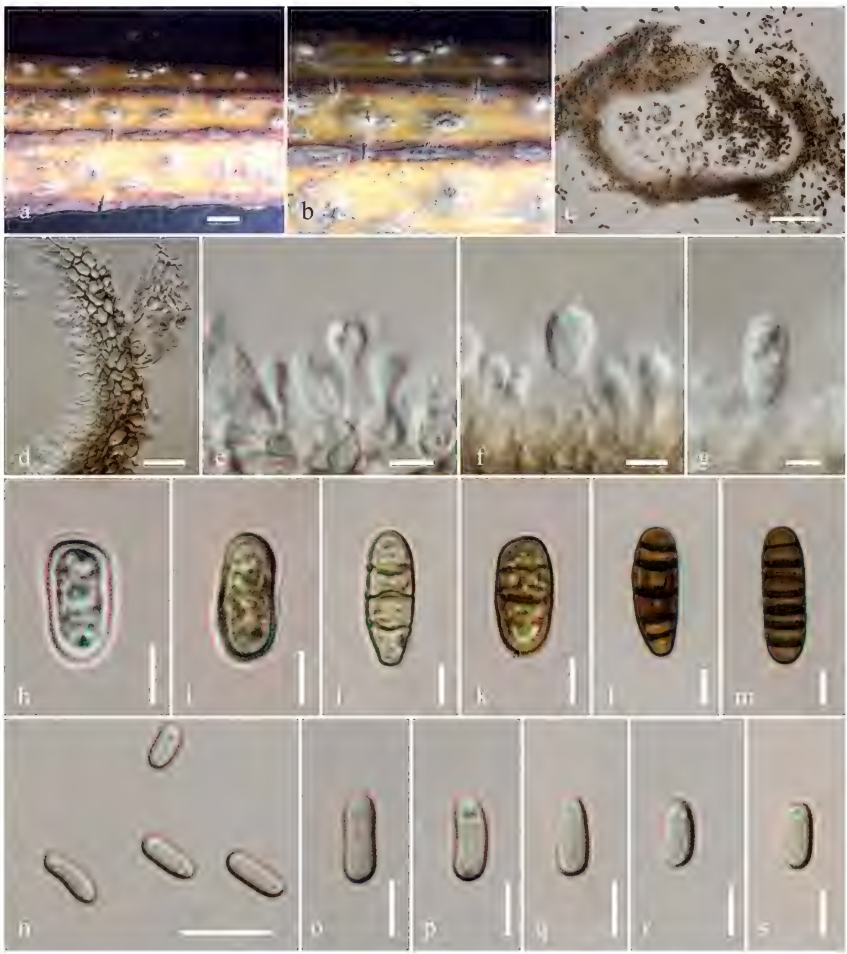


PLATE. 4. *Camarosporidiella halimodendri* (MFLU 17-2008). a, b. Conidiomata on host surface; Conidioma, vertical section; d. Peridium; e–g. Conidiogenous cells; h–m. Macroconidia; n–s. Microconidia. Scale bars: a, b = 1000 µm; c = 100 µm; d = 30 µm; e–m, o–s = 5 µm; n = 10 µm.

macroconidiogenous cells, hyaline, distinct, enteroblastic, annellidic, ampulliform to subcylindrical. MICROCONIDIA 6.6–10.4 × 2.5–3.3 µm (x = 7.9 × 3.0 µm, n = 20), hyaline, oblong to ellipsoidal, allantoid, with a few small guttules, smooth-walled.

Culture Characteristics: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with sparse mycelium, circular, smooth well-defined margin, grey in the middle, white in the edges, reverse cream-grey in the middle, whitish at the edge, flat on the surface.

Specimen examined: **RUSSIA, Rostov region, Shakhty city district**, urban artificial forest, on dying twigs of *Robinia pseudoacacia*, 26 May 2017, Timur S. Bulgakov (MFLU 17-2008; living cultures MFLUCC 18-0767, DSM 109977).

Notes: Our new isolate MFLUCC 18-0767 shares a close phylogenetic affinity to *Camarosporidiella halimodendri* (MFLUCC 14-0905) in our combined LSU, SSU, ITS, and TEF phylogenetic tree. Our isolate differs slightly morphologically from the type description in microconidial shape and larger size (vs. 4.5–7.5 × 3.5–4.5 µm). *Camarosporidiella halimodendri* has not previously been reported from *Robinia pseudoacacia*, reported here as a new host.

Hosts: *Caragana frutex*, *C. halodendron* (Pall.) Dum. Cours. [≡ *Halimodendron halodendron* (Pall.) Voss], *Cytisus podolicus* Blocki [≡ *Chamaecytisus podolicus* (Blocki) Klásk.], *Lycium barbarum* L. (Wanasinghe & al. 2017), *Robinia pseudoacacia* (this study).

Distribution: Russia: Wanasinghe & al. 2017, this study.

Camarosporidiella moricola (Chethana, Bulgakov & K.D. Hyde) Wanas. & K.D. Hyde, Stud. Mycol. 87: 238 (2017) Plate 5, Fig. 2k,l

Necrotrophic on dead and dying twigs of *Morus nigra* L. (*Moraceae*).

Sexual morph: Undetermined.

Asexual morph: Conidiomata 110–175 µm diam., 210–290 µm high, pycnidial, solitary, scattered, semi-immersed, unilocular, globose, black, with a papillate ostiole. Conidiomatal wall 15–30 µm thick at the base, 20–30 µm thick at the sides, multi-layered, outer layer composed of 3–4 layers of thick, dark brown cells; inner 4–6 layers hyaline cells of textura angularis. Conidiophores reduced to conidiogenous cells. Conidiogenous cells enteroblastic, with percurrent annellations, doliiform, hyaline, smooth-walled, formed from the inner most layer of the conidiomatal wall. Conidia 11–12 × 4–5 µm (x = 11.9 × 5.3 µm, n = 20), oblong, ellipsoidal, straight to slightly curved, initially hyaline becoming pale to dark brown at maturity, smooth-walled, rounded at both ends, muriform, 1–3-transversely septate and 1–2 vertical septa.

Culture Characteristics: Mycelium slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with dense mycelium, circular, fimbriate,

Plate. 5. *Camarosporidiella moricola* (MFLU 17-0991). a, b. Conidiomata on host surface; c. Conidioma, vertical section; d. Peridium; e–g. Conidiogenous cells and developing conidia; h–m. Conidia. Scale bars: a = 500 µm; b = 300 µm; c = 50 µm; d = 40 µm; e–g = 5 µm; h–m = 10 µm.

rough margin, olivaceous grey in the middle, reverse creamy-white, flat on the surface.

Specimens examined: **ITALY, province of Forlì-Cesena, Predappio Alta–Predappio**, on dead branch of *Morus nigra*, 5 May 2017, Erio Camporesi (MFLU 17-0991, MFLUCC 17-2310); **RUSSIA, Rostov region, Shakhty city**, urban artificial forest, on *Morus alba*, 26 May 2017, Timur S. Bulgakov (MFLU 17-2060; living cultures MFLUCC 18-0771, DSM 109975); **Shakhty city district**, artificial forest, on dead twigs of *Morus alba*, 11 June 2017, Timur S. Bulgakov (MFLU 17-2036; living cultures MFLUCC 18-0770, DSM 109835); trees near Atyukhta river, on dead twigs of *Morus alba*, 1 June 2017, Timur S. Bulgakov (MFLU 17-1904; living cultures MFLUCC 18-0766, DSM 109917); block green belt, on *Morus alba*, 8 May 2017, Timur S. Bulgakov (MFLU 17-2085; living cultures MFLUCC 18-0772, DSM 109795); Hospital park, trees, on dead twigs of *Morus alba*, 3 June 2017, Timur S.

Bulgakov (MFLU 17-2010; living cultures MFLUCC 18-0768, DSM 109792); former Shakhty Forest, artificial forest, on dead twigs of *Morus alba*, 11 June 2017, Timur S. Bulgakov (MFLU 17-2035; living cultures MFLUCC 18-0769, DSM 109976).

Notes: Multi-gene phylogenetic analyses group MFLU 17-2310, MFLUCC 18-0766, MFLUCC 18-0768, MFLUCC 18-0769, MFLUCC 18-0770, MFLUCC 18-0771, MFLUCC 18-0772 with *Camarosporidiella moricola*. A BLASTn search of LSU, SSU, ITS, TEF sequences places the seven strains at 99–100% similarity with *C. moricola*. The *C. moricola* type strain differs from our specimens in its larger (150–340 µm diam.) conidiomata. *Camarosporidiella moricola* has been described only on *Morus* species from Russia. We examined fresh specimens both from Russia and Italy. We identify our strains as *C. moricola* and report MFLU 17-0991 as new for Italy.

Hosts: *Morus alba* (Tibpromma & al. 2017, Wanasinghe & al. 2017); *Morus nigra* (this study).

Distribution: Russia (Tibpromma & al. 2017, Wanasinghe & al. 2017), Italy (this study).

Camarosporidiella robiniicola (Wijayaw., Camporesi & K.D. Hyde) Wijayaw., Wanas. & K.D. Hyde, Stud. Mycol. 87: 241 (2017) Plate 6, Fig. 2i,j

Necrotrophic on dying and dead branches of *Robinia pseudoacacia*.

Sexual morph: Undetermined.

Asexual morph: Conidiomata pycnidial, 500–700 µm diam., 200–450 µm high, solitary or gregarious, black, immersed, unilocular, papillate. Conidiomatal wall multi-layered, 20–35 µm thick at the base, 10–25 µm thick at the sides, comprising 4–5 layers of dark brown cells of textura angularis, with lighter cells towards the inside, inner layer composed of 2–4 layers, hyaline, thin-walled cells of textura angularis. Conidiophores reduced to conidiogenous cells. Conidiogenous cells enteroblastic, annellidic, doliiform, obclavate, hyaline, smooth. Conidia 16–20 × 7–9 µm (x = 18.2 × 8.2 µm, n = 20), oblong, straight to slightly curved, rounded at both ends, 4–6-transversely septate, with 1 vertical septum, muriform, smooth, initially pale brown becoming dark brown on maturity.

Culture Characteristics: Slow growing, reaching 3 cm diam. after 4 weeks at 25°C, later with sparse dense mycelium, off-white to white in the middle, white in the edge, circular, smooth, slightly irregular margin, thin mycelia, radially furrowed, reverse creamy to off-white, flat on the surface.

Specimens examined: **UKRAINE, Donetsk region, Donetsk city,** Donetsk Botanical Garden, arboretum, on dying twigs and branches of *Robinia pseudoacacia*,

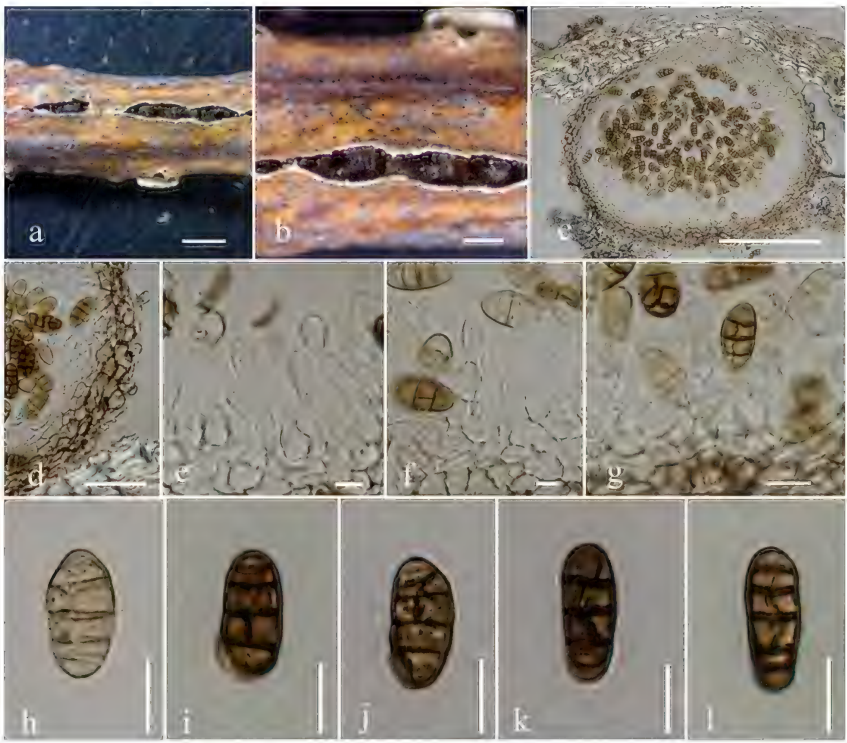


Plate. 6. *Camarosporidiella robiniicola* (MFLU 17-2469). a, b. Conidiomata on host surface; c. Conidioma, vertical section; d. Peridium; e–g. Conidiogenous cells and developing conidia; h–l. Conidia. Scale bars: a, b = 1000 μm; c = 50 μm; d, h–l = 10 μm; e, f = 5 μm; g = 15 μm.

18 May 2017, Timur S. Bulgakov (MFLU 17-2469; living cultures MFLUCC 18-0775); **RUSSIA, Rostov region, Shakhty city district**, Alexandrovsky (Central) Park, trees, on dead twigs of *Robinia pseudoacacia*, 5 November 2017, Timur S. Bulgakov (MFLU 18-0320; living cultures MFLUCC 18-0789; DSM 109791).

Notes: The isolate MFLUCC 18-0775 clustered with *Camarosporidiella robiniicola* with moderate bootstrap support (ML = 70%, BI = 1). The type species as described by Wijayawardene & al. (2014) differs morphologically from our specimen in its smaller conidiomata (210–240 × 180–220 μm).

Hosts: *Gleditsia triacanthos*, *Robinia neomexicana* (Wijayawardene & al. 2014, Wanasinghe & al. 2017), *R. pseudoacacia* (this study)

Distribution: Italy (Wijayawardene & al. 2014, Wanasinghe & al. 2017), Ukraine and Russia (this study).

Discussion

Morphological circumscription and phylogeny

All phylogenetic analyses show that *Camarosporidiella* is monophyletic as traditionally circumscribed, but not all clades are well supported. Phylogenies derived herein are consistent with those of Wanasinghe & al. (2017), who sampled 99 *Camarosporidiella* strains.

Camarosporidiella moricola (Clade A) and *C. robiniicola* (Clade B) isolates cluster in two clades. These two species produce morphologically similar conidia: oblong, ellipsoidal, and pale to dark brown. However, in *C. moricola,* conidiomata appear as small black dots, semi-immersed on the substrate while those of *C. robiniicola* are completely immersed in the substrate. Conidia of *C. robiniicola* are larger (18–28 × 7–11 µm) than in *C. moricola* (8–15 × 4–7.5 µm) and differ in the number of septa—4–6 transverse septa, 1 vertical septum vs. 1–3 transverse septa, 1–2 vertical septa. ITS and TEF sequences are similar for the two species in this study.

Clade C, which shares a common geographical distribution, comprises *Camarosporidiella clematidis*, *C. elongata*, *C. eufemiana*, *C. laburni*, *C. laburnicola*, *C. mirabellensis*, *C. premilcurensis*, *C. spartii*, and one unidentified isolate (*Camarosporidiella* sp. CPC 12441). Morphological dimensions within this clade overlap for ascomata (650–950 µm × 500–775 µm), asci (130–255 µm ×14–18 µm), and ascospores (20–38 µm × 8–12 µm). However, the species can be distinguished by the number of septa (Table 2). There are only <0.5% ITS base pair (bp) differences and <0.8% TEF bp differences separating the species.

Clade D sequences represent two species: *Camarosporidiella celtidis* and *C. populina*. Hyde & al. (2018) separated *C. populina* by its smaller and superficial to semi-immersed conidiomata, phialidic conidiogenous cells, and larger 1–3 transversely septate conidia from *C. celtidis* with larger immersed conidiomata; annellidic integrated conidiogenous cells, and smaller conidia with 2–3 transverse septa and one vertical septum. Nonetheless, only two bp differences separate the *C. populina* and *C. celtidis* ITS sequences. There is no TEF sequence available for *C. populina*. Whether *C. populina* is a separate species warrants further investigation.

Clade E comprises *Camarosporidiella elaeagnicola*. All isolates within the clade are morphologically similar. Our isolate (MFLUCC 18-0782) is morphologically slightly different in having smaller conidiomata and shorter conidia from other species of *C. elaeagnicola* within the clade. But

comparison of ITS and TEF sequences shows no nucleotide bp differences among the species.

Clade F, which comprises the four species *Camarosporidiella caraganicola*, *C. mori*, *C. melnikii*, and *C. italica,* are distinguished by conidiomatal and ascomatal sizes and the morphology of asci, conidia, and ascospores.

Camarosporidiella caraganicola, isolated from dead branches of *Coronilla emerus*, is morphologically similar to *C. italica* in cylindrical asci measuring 150–190 × 10–15 µm (Wanasinghe & al. 2017), but differs in its smaller ascospores (20–30 × 7–10 µm vs. 30–35 × 12–14 µm) and its 3–5 transverse septa, 2–4 vertical septa (vs. 6–8 transverse septa, 2–3 vertical septa in *C. italica*). Within clade F the ITS region of *C. caraganicola* has 10 (1.8%; *C. melnikii*), 3 (0.7%; *C. mori*), and 9 (1.6%; *C. italica*) bp differences, and the TEF region comparison between *C. caraganicola* to that of 5 (0.5%; *C. melnikii*) and 11 (1.2%; *C. italica*) bp differences. No TEF data is available for *C. mori*. *Camarosporidiella mori,* which was isolated from *Morus alba,* shares a conidial size range (15.5–21 × 6.5–9.5 µm) with *C. celtidis* and *C. schulzeri.* However, within clade F *C. mori* is phylogenetically distant from *C. celtidis* and *C. schulzeri*, clustering closer to *C. italica*. The *C. mori* ITS sequence shows a 1.7% bp difference to *C. celtidis*, a 1.6% bp difference to *C. schulzeri,* and a 1.3% (7) bp) difference to *C. melnikii* and *C. italica*. Although *Camarosporidiella melnikii,* morphologically distinct from *C. caraganicola* and *C. italica*, closely resembles *C. celtidis* in its muriform ascospores measuring 11–16 × 5–6 µm with 2–3 transverse septa and without vertical septa, it is phylogenetically separate from *C. celtidis* with 6 (1.1%) ITS and 8 (0.9%) TEF bp differences; *C. melnikii* shows 9 (1.6%) ITS and 11 (1.2%) TEF bp differences from *C. italica*.

The *Camarosporidiella schulzeri* isolates form the monophyletic Clade G (Fig. 1c); *C. schulzeri* resembles *C. elaeagnicola* in its black, immersed 300–500 × 300–550 µm conidiomata and similarly sized conidia (15–21 × 8–12 µm vs. 18–25 × 9–13 µm), both with 2–3 transverse septa and 1 vertical septum. *Camarosporidiella schulzeri* shows 1.06% ITS and 1.12% TEF bp differences to *C. elaeagnicola*, which supports the two species as phylogenetically distinct.

Sequences representing *Camarosporidiella halimodendri*, *C. arezzoensis* and *C. aborescentis,* which form distinct monophyletic groups as clade H, clade I, and clade J, are morphologically similar and phylogenetically close. In addition, there are no bp differences in the ITS and TEF sequences among the three clades.

Table 2a. Sexual stage morphology

Clade	Species	Sexual stage morphology (µm)				Reference
		Ascomata (µm)	Asci (µm)	Ascospores (µm)	Septa (TS[b], LS[c])	
A	*C. moricola*	Undetermined				T
B	*C. robiniicola*	Undetermined				Wi
C	*C. clematidis*	Undetermined				Wi
	C. elongata	650–950 × 500–775	140–255 × 14–18	21–38 × 8–12	3–8 TS, 5–7 LS	Wa
	C. eufemiana	350–400 × 450–550	130–150 × 14–15	20–25 × 10–12	3–5 TS, 1 LS	Wa
	C. laburni	400–550 × 500–600	160–190 × 12–16	27–32 × 10–12	6–7 TS, 1–2 LS	Wa
	C. mirabellensis	300–350 × 500–550	140–170 × 12–16	22–27 × 9–11	3–5 TS, 1–2 LS	Wa
	C. premilcurensis	400–450 × 500–600	160–210 × 14–16	22–27 × 10–12	5–7 TS, 1–2 LS	Wa
	C. laburnicola	280–370 × 220–320	125–150 × 9–11	15–21 × 6–8	6–7 TS, 5–6 LS	T
D	*C. spartii*	Undetermined				Wi
	C. celtidis	200–400 ×300–475	120–160 × 12–15	19.9 × 7.9	3–5 TS, 1–2(–3) LS	Th, Wa
	C. populina	Undetermined				H
E	*C. elaeagnicola*	Undetermined				Wa
F	*C. caraganicola*	400–550 × 450–500	150–190 × 10–15	20–30 × 7–10	3–5 TS, 2–4 LS	L
	C. italica	400–450 × 550–600	150–180 × 15–20	30–35 × 12–14		Wa
	C. melnikii	Undetermined				Wa
	C. mori	Undetermined				H
G	*C. schulzeri*	Undetermined				Wa
H	*C. halimodendri*	Undetermined				Wa
I	*C. arezzoensis*	400–500 × 450–550	180–240 × 10–15	19–28 × 9–15	5–7 TS, 4–6 LS	Wa
J	*C. aborescentis*	350–450 × 500–600	170–210 × 15–18	28–32 × 12–13	5–7 TS, 1–2 LS	L
K	*C. mackenziei*	500–750 µm diam	131–210 × 15–16	30–35 × 10–12.5	5–6 TS, 1 LS	Wa

[a] Reference abbreviations: C = Crous & al. (2018); H = Hyde & al. (2019); L = Liu & al. (2015); T = Tibpromma & al. (2017); Th = Thambugala & al. (2016); Wa = Wanasinghe & al. (2017); Wi = Wijayawardene & al. (2014).

[b]TS: Transverse septa; [c]LS: Longitudinal septa.

Table 2b. Asexual stage morphology

Clade	Species	Asexual stage morphology (µm)				Reference
		Conidiomata (µm)	Conidia (µm)	Microconidia (µm)	Septa (TS, LS)	
A	*C. moricola*	150–340 diam.	8–15 × 4–7.5		1–3 TS, 1–2 VS	T
B	*C. robiniicola*	180–220 × 210–240	18–28 × 7–11		4–6 TS, 1 VS	Wi
C	*C. clematidis*	350–380 × 370–425	10–17 × 7–9		2–3 TS, 1 VS	Wi
	C. elongata	400–500 diam.	13–21 × 7–10			Wa
	C. eufemiana		Undetermined			Wa
	C. laburni	300–350 × 300–400	20–30 × 8–11		4–5 TS, 1–2 VS	Wa
	C. laburnicola		Undetermined			T
	C. mirabellensis		Undetermined			Wa
	C. premilcurensis		Undetermined			Wa
D	*C. spartii*	200–225 × 250–300	13–16 × 6–7		3–4 TS, 2–3 VS	Wi
	C. celtidis	300–350 × 350–450	15–20 × 6–8		2–3 TS, 0 VS	Th, Wa
	C. populina	200–360 diam.	11– 17 × 4–7		1–3 TS, 1 VS	H
E	*C. elaeagnicola*	300–500 × 300–550	18–25 × 9–13	5–6.5 × 3.5–4.5	2–3 TS, 1 VS	Wa
F	*C. caraganicola*	413–604 × 280–780	13–26 × 6–13		1–4 TS, 1–4 VS	L
	C. italica		Undetermined			Wa
	C. melnikii	350–550 × 300–500	11–16 × 5–6	7–12 × 4–7	2–3 TS, 0 VS	Wa
	C. mori	370–520 × 220–430	15.5–21 × 6.5–9.5		4 TS, 1 VS	H
G	*C. schulzeri*	370–420 × 380–460	15–21 × 8–12	4.5–6.5 × 4.5–5.5	2–3 TS, 1 VS	Wa
H	*C. halimodendri*	500–600 × 350–600	18–25 × 8–12	4.5–7.5 × 3.5–4.5	4–6 TS, 1–2 VS	Wa
I	*C. arezzoensis*	300–400 × 300–350	20–28 × 6–9	5–7.5 × 3.5–4.5	4–7 TS, 1–2 VS	Wa
J	*C. aborescentis*	350–600 × 490– 770	12–25 × 5–13		1–3 TS, 1–4 VS	L
K	*C. mackenziei*	450–550 × 500–600	17–25 × 9–13	6.5–8 × 4–6	3–4 TS, 1–2 VS	Wa

[a] Reference abbreviations: see Table 2a footnote.

Table 2c. Host substrata per clade/species

Clade	Species	Hosts
A	*C. moricola*	*Morus alba*, *M. nigra* (*Moraceae*)
B	*C. robiniicola*	*Gleditsia triacanthos*, *Robinia neomexicana*, *R. pseudoacacia* (*Fabaceae*)
C	*C. clematidis*	*Clematis vitalba* (*Ranunculaceae*)
	C. elongata	*Cytisus scoparius*, *Robinia pseudoacacia* (*Fabaceae*)
	C. eufemiana	*Cytisus* sp. (*Fabaceae*)
	C. laburni	*Laburnum anagyroides* (*Fabaceae*)
	C. laburnicola	*Laburnum anagyroides* (*Fabaceae*)
	C. mirabellensis	*Robinia pseudoacacia* (*Fabaceae*)
	C. premilcurensis	*Cytisus* sp. (*Fabaceae*)
D	*C. spartii*	*Bassia* sp. (*Amaranthaceae*), *Cytisus* sp. (*Fabaceae*)
	C. celtidis	*Ailanthus altissima* (*Simaroubaceae*), *Betula pendula* (*Betulaceae*), *Celtis occidentalis* (*Cannabaceae*)., *Elymus repens* (*Poaceae*), *Gleditsia triacanthos* (*Fabaceae*), *Maclura pomifera*, *Morus alba* (*Moraceae*), *Prunus padus*, *Robinia* sp., *Spiraea* sp (*Rosaceae*), *Ulmus pumila* (*Ulmaceae*).
	C. populina	*Populus nigra* var. *italica* (*Salicaceae*)
E	*C. elaeagnicola*	*Artemisia santonicum* (*Asteraceae*), *Cytisus ruthenicus* (*Fabaceae*), *Elaeagnus angustifolia* (*Elaeagnaceae*)
F	*C. caraganicola*	*Amorpha fruticosa*, *Caragana frutex* (*Fabaceae*)
	C. italica	*Hippocrepis emerus* (*Fabaceae*)
	C. melnikii	*Caragana frutex* (*Fabaceae*)
	C. mori	*Morus alba*, *M. nigra* (*Moraceae*)
G	*C. schulzeri*	*Gleditsia triacanthos*, *Elaeagnus angustifolia* (*Fabaceae*)
H	*C. halimodendri*	*Caragana frutex*, *C. halodendron*, *Cytisus podolicus*, *Robinia pseudoacacia* (*Fabaceae*), *Lycium barbarum* (*Solanaceae*)
I	*C. arezzoensis*	*Amorpha* sp., *Cytisus* sp. (*Fabaceae*)
J	*C. aborescentis*	*Colutea arborescens*, *C. orientalis*, *Cytisus borysthenicus* (*Fabaceae*)
K	*C. mackenziei*	*Caragana arborescens*, *Caragana* sp. (*Fabaceae*)

Clade K comprises isolates representing *Camarosporidiella mackenziei* and two previously unidentified species. *Camarosporidiella mackenziei* was previously isolated from *Caragana arborescens* from south European Russia. While there are no ITS bp differences separating *C. mackenziei* and *Camarosporidiella* sp. CPC 25960 and CPC 25962, TEF comparisons reveal

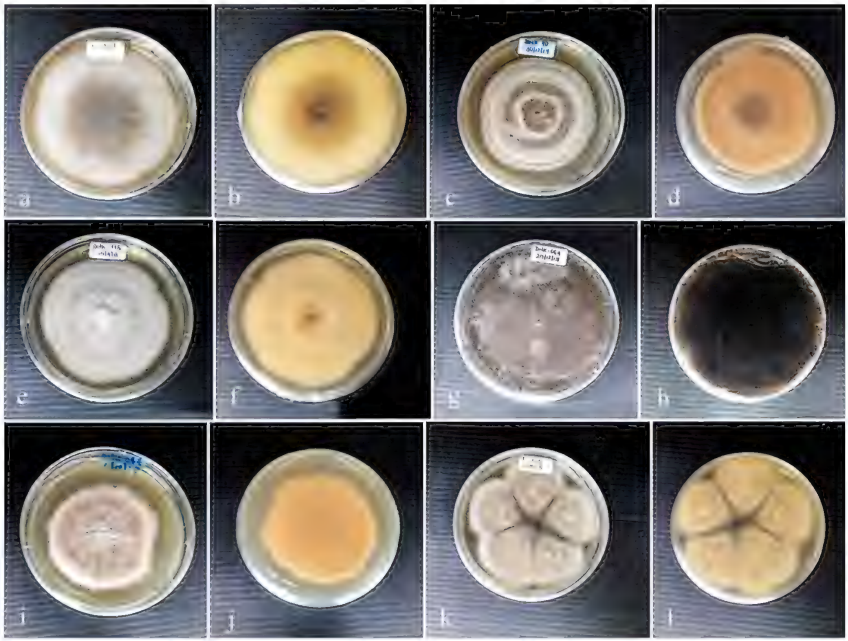


FIG. 2. *Camarosporidiella* spp. cultures. a, b: ***C. halimodendri***. c, d: ***C. celtidis***. e, f: ***C. caraganicola***. g, h: ***C. elaeagnicola***. i, j: ***C. robiniicola***. k, l: ***C. moricola***.

a 0.77% (7) bp difference with CPC 25960 and 0.66% (6 bp) difference with CPC 25962. Recently, Crous & al. (2018), who described the sexual morph of *C. mackenziei,* identified CPC 25960 and CPC 25962 (isolated from *Caragana* sp. in Finland) as *C. mackenziei*.

Identification of *Camarosporidiella* species using ITS region can be challenging, as it does not contain sufficient variation for distinguishing between species, although it is useful in BLAST searches of the NCBI database to get information on species clusters and to confirm new sequences against curated sequences (Doilom & al. 2017). Nonetheless, in this study, ITS-based phylogenies resolved the clades (data not shown) very well, even while pairwise alignment revealed very little difference (<1%) among species. The TEF region, which has been widely used in the taxonomy and systematics of *Camarosporidiella* (Liu & al. 2017, Tibpromma & al. 2017, Wanasinghe & al. 2017), provided better resolution for species-level identification (data

not shown). Yet, bp differences among TEF sequences across species were likewise very small (< 1%). Therefore, using the ITS marker alone to identify *Camarosporidiella* species is probably not sufficient, requiring protein-coding gene sequences as well. A RPB2-based phylogeny might give better results and greater bp differences among species compared to TEF. Further studies are required to see whether amplifying RPB2 gene fragments is possible and useful for identifying *Camarosporidiella* species. If so, we encourage researchers to deposit *Camarosporidiella* RPB2 sequence data in GenBank.

Diversity and host association

Camarosporidiella species are distributed over a wide host range, with higher percentages in *Fabaceae* (45%), *Moraceae* (22%), and *Elaeagnaceae* (12%) (Fig. 3). Most species have been named based on the host from which the fungus was isolated. In the present study, *C. caraganicola*, *C. celtidis* and *C. halimodendri* comprise new host records for Russia. One of our isolates, MFLUCC 18-0786,

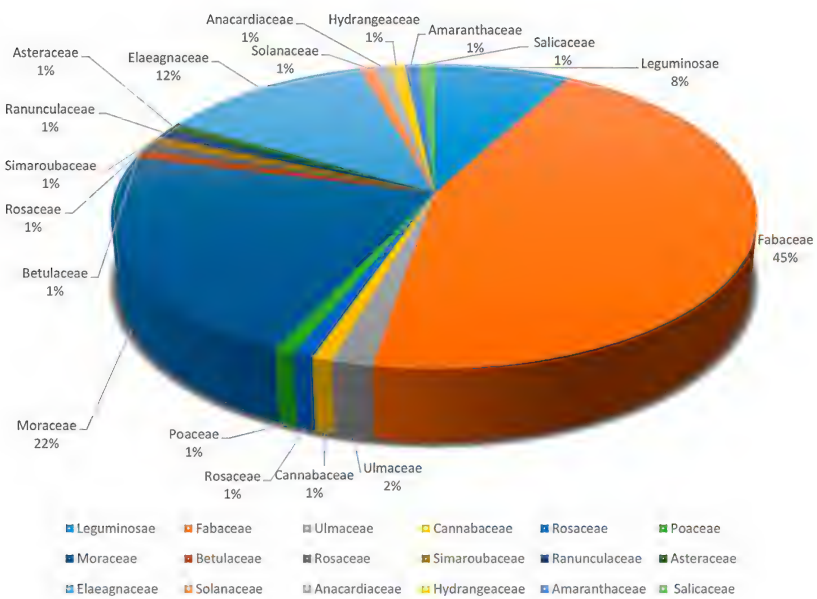


Fig 3. Family affiliations of hosts of *Camarosporidiella* strains with molecular data.

clustered in Clade F (Fig. 1) among *Camarosporidiella caraganicola* sequences. We add a new host to the fungal records from *Fabaceae* as *C. caraganicola* has not been previously reported on *Amorpha fruticosa*. The morphology of *C. caraganicola* MFLUCC 18-0786 fully agree with the descriptions provided by Liu & al. (2015) and Wanasinghe & al. (2017).

Camarosporidiella celtidis, previously described as *Cucurbitaria celtidis* by Shear (1902), was previously isolated from *Celtis occidentalis* in Osborne, Kansas. The species was transferred to *Camarosporium* by Thambugala & al. (2016) based on molecular data from a fresh collection. *Cucurbitaria celtidis* was later re-circumscribed as *Camarosporidiella celtidis* by Wanasinghe & al. (2017), who illustrated its asexual morph. *Camarosporidiella celtidis* has been reported on a wide range of hosts including *Celtis occidentalis* (*Cannabaceae*), *Gleditsia triacanthos* (*Fabaceae*), *Maclura pomifera* (*Moraceae*), *Spiraea* sp. (*Rosaceae*), *Prunus padus* (*Rosaceae*), *Morus alba* (*Moraceae*), *Elymus repens* (*Poaceae*), *Betula pendula* (*Betulaceae*), and *Ailanthus altissima* (*Simaroubaceae*) (Ellis & Everhart 1894, Shear 1902, Thambugala & al. 2016, Wanasinghe & al. 2017). In the present study, *C. celtidis* was recovered from dead *Ulmus pumila* twigs in Ukraine. Our new isolate also matches the descriptions of Wanasinghe & al. (2017).

Likewise, *Camarosporidiella halimodendri* has been collected in Iran by Farr & Rossman (2017). The isolate *C. halimodendri* (MFLUCC 18-0767) from *Robinia pseudoacacia* clustered in Clade H with other *C. halimodendri* isolates. We found no description for *C. halimodendri* isolates from *Robinia pseudoacacia* in any scientific publication. From previous studies, we know that phenotypic variation often depends on host substrata, environmental conditions, and geographical location (Jain & Fries 2009, Hewitt & al. 2016, Elliot & al. 2018, De Silva & al. 2016, Promputtha & al. 2019). We should note that MFLUCC 18-0767 morphologically differs slightly from the other *C. halimodendri* in this clade in its shorter conidia and different microconidia.

Camarosporidiella elaeagnicola has been collected on *Elaeagnus angustifolia* from Russia and from *E. rhamnoides* in Germany. We regard our three isolates grouped in Clade E as representing additional collections of *C. elaeagnicola*. *Camarosporidiella*

robiniicola, previously collected from *Robinia pseudoacacia* in Italy, was first described by Wijayawardene & al. (2014), and later Wanasinghe & al. (2017) reported additional collections by adding seven new C. *robiniicola* strains; here we present our two isolates in Clade B as representing new collections of *C. robiniicola* from Russia. *Camarosporidiella moricola* was originally proposed in Tibpromma & al. (2017; as *Camarosporium moricola*), and Wanasinghe & al. (2017) added twelve strains collected from *Morus alba* in Russia. We identifiy our six strains MFLUCC 18-0766, MFLUCC 18-0768, MFLUCC 18-0769, MFLUCC 18-0770, MFLUCC 18-0771, and MFLUCC 18-0772 (also from Russia) and MFLU 17-0991 (a new record from Italy on *Morus nigra*) as *C. moricola* based on cultural and morphological characteristics.

Our current data indicate greater species diversity and a much wider range of habitat for *Camarosporidiella* species in many countries of the northern hemisphere. It is very likely that many *Camarosporidiellaceae* were initially described as species in *Camarosporium* s. lat., as other anamorphic fungi with pigmented septate conidia (e.g., *Dichomera*, *Hendersonia*), or their sexual stages as ascomycetes with pigmented septate ascospores (e.g., *Cucurbitaria*, *Pleospora*). For example, 78 *Camarosporium* spp., 3 *Dichomera* spp., 54 *Hendersonia* spp., and 48 *Cucurbitaria* spp. were previously recorded on Ukraine territory alone (Andrianova & al. 2006), many of which on the same host plant species now cited for *Camarosporidiella* species collected in the adjacent Rostov region of Russia. Undoubtedly at least some of those fungi and *Camarosporidiella* species are conspecific. Unfortunately, the original species descriptions of most species in *Camarosporium*, *Dichomera*, and *Hendersonia* are very brief, incomplete, and sometimes even controversial. Therefore, it is difficult to compare species described in the 21st century with 19th and 20th century descriptions based solely on morphological features.

Camarosporidiella species are mainly saprobic on dead twigs and branches of woody plants, with some being necrotrophic pathogens causing necroses of twigs and branches of woody angiosperms. This implies a rather wide host specialization for the pathogenic species. Although most *Camarosporidiella* species were named based on the host plant from which they were isolated for the first time, it is

already clear that many species (especially saprobic) can potentially grow on angiosperms of many genera, families, orders, and classes. Nevertheless, our observations indicate that each *Camarosporidiella* species usually colonizes plants of a certain plant genus or plant family, although many species may colonize closely related (or even not so closely related) woody plants. Occasionally different *Camarosporidiella* species coexist on the same plant species, often simultaneously on the same plant.

For example, *Camarosporidiella caraganicola*, *C. halimodendri,* and *C. melnikii* were all found on *Caragana frutex; C. robiniicola* and *C. schulzeri* were both found on *Gleditsia triacanthos;* and *Camarosporidiella mirabellensis*, *C. robiniicola,* and *C. schulzeri* were found on *Robinia pseudoacacia* in Russia and Italy (Wanasinghe & al. 2017). *Camarosporidiella robiniicola* was found not only on its primary hosts (*Robinia pseudoacacia* and other *Robinia* spp.), but also on another closely related leguminous tree—*Gleditsia triacanthos* (Wanasinghe & al. 2017) as well as an unrelated introduced shrub *Cotinus coggygria* Scop. (Liu & al. 2015) growing under *Robinia pseudoacacia.* In this study, we found *Camarosporidiella caraganicola* on an *Amorpha fruticosa* surrounded by *Caragana frutex* shrubs. *Camarosporidiella elaeagnicola* was found not only on its main host plant (*Elaeagnus angustifolia*), but also on the aboriginal dwarf semi-shrub *Artemisia santonica* (Wanasinghe & al. 2017), aboriginal low shrub *Cytisus ruthenicus,* and introduced *Robinia pseudoacacia* (this study); but in all cases those new host plants were located close to *Elaeagnus angustifolia* trees affected by *Camarosporidiella elaeagnicola*.

We hypothesize that many necrotrophic *Camarosporidiella* species move from main host plants to nearest closely related and even distantly related plants, especially when growing together in botanical gardens, arboreta, artificial forests, urban parks, and private gardens. Saprobic *Camarosporidiella* species therefore can grow on very wide range of host plants. For example, saprobic *C. celtidis* was found on many plants of many families, so we could expect the species to be found on dead stems, twigs, and branches of many other plant species. It is likely that *C. celtidis* was first recorded as *Hendersonia sarmentorum* Westend. or some other *Hendersonia* species in Ukraine (Andrianova & al. 2006).

It is notable that the hosts of many *Camarosporidiella* species originate in North America (*Amorpha fruticosa*, *Celtis occidentalis*, *Gleditsia triacanthos*, *Robinia pseudoacacia*, *R. neomexicana*), Central Asia (*Caragana halodendron*, *Elaeagnus angustifolia*, *Morus nigra*), and East Asia (*Ailanthus altissima*, *Caragana arborescens*, *Cotinus coggygria*, *Lycium barbarum*, *Morus alba*). These plants were introduced to many European countries (including Italy and Russia) over a century ago, and today many have become invasive in some regions of Russia (The Black Data Book of the flora of Central Russia 2009) and Europe (DAISIE 2009). Because of their obligate associations with alien plants, many *Camarosporidiella* species might also be treated as alien fungal species in territories where they are found for the first time.

Many *Camarosporidiella* species were both weakly supported in our phylogenetic analyses and morphologically similar. We also cannot rely on cultural variation or on morphological descriptions of specimens collected in the 19th–20th centuries to delimit species. *Camarosporidiella* is a complex taxonomic group requiring integrative taxonomy rather than phylogenies based only on neutral markers (Zamora & al. 2015, Caparrós & al. 2016, Hyde & al. 2020, Jayasiri & al. 2017, Konta & al. 2020, Sharma & al. 2016). For these reasons, new specimen collections and further research on *Camarosporidiella* in Europe, Central and East Asia, and North America are needed to clarity the origins of many species, their natural diversity, and relationships.

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Compliance with ethical standards. There is no conflict of interest (financial or non-financial) and all authors have agreed to submission of the paper. The authors also declare that they have no conflict of interest and confirm that the field studies did not involve endangered or protected species.

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Microbotryum bardanense and *M. polygoni-alati* —new records from Nepal

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Abstract—Two smut fungi, *Microbotryum bardanense* and *M. polygoni-alati,* are reported for the first time from Nepal. Descriptions, illustrations, and taxonomic notes are provided for these taxa.

Key words—*Caryophyllaceae, Microbotryaceae, Persicaria nepalensis, Polygonaceae, Silene moorcroftiana*

Introduction

In its broad circumscription, *Microbotryum* Lév. comprises 99 species (Kemler & al. 2020). This genus has a nearly world-wide range, but many of its species are known from one or a limited number of localities (Vánky 2011, 2013). Some of them are undoubtedly under-recorded and in need of additional distribution data, especially from some understudied regions of the world, such as the Himalayas.

During examinations in the herbarium of the Royal Botanic Garden Edinburgh, UK (E) and T.B. Lee Herbarium in College of Agriculture and Life Sciences, Seoul National University, Seoul, Korea (SNUA), carried out by one of the authors (CMD), some specimens from Nepal, infected by smut fungi, were found. Two rarely collected smut fungi, *Microbotryum bardanense* and *M. polygoni-alati,* are reported here for the first time from Nepal.

Materials & methods

Dried specimens from E and SNUA were examined under light microscope (LM) and scanning electron microscope (SEM). For LM observations and measurements, spores were mounted in lactoglycerol solution (w : la : gl = 1 : 1 : 2) on glass slides, gently heated to boiling point to rehydrate the spores, and then cooled. The spore measurements are given as min–max (mean ± standard deviation). For SEM, spores were attached to specimen holders by double-sided adhesive tape and coated with gold in an ion sputter. The surface structure of spores was observed and photographed at 10 kV accelerating voltage using a JEOL SM-6390 scanning electron microscope. The height of warts was measured in LM. The descriptions below are based entirely on the specimens examined. The lists of shapes of spores are arranged in descending order of frequency.

Taxonomy

Microbotryum bardanense Chleb. & Suková, Mycotaxon 93: 150, 2005. FIG. 1

INFECTION systemic. SORI in considerably swollen anthers, filling pollen sacs with a pulverulent, dark brick (based on Rayner 1970) or purplish date (based on the Colour identification chart of Anonymous 1969) spore mass. SPORES subglobose, globose, broadly ellipsoidal or ovoid, sometimes ellipsoidal, (5–)5.5–7(–8) × (4.5–)5–6.5(–7) µm (6.4 ± 0.5 × 5.8 ± 0.4 µm) (n = 100), light vinaceous; wall irregularly, moderately verruculose to incompletely reticulate, 0.7–1.1 µm thick, including 0.3–0.5 µm high ornamentation. In SEM, spore wall moderately echinulate-verruculose, ornaments often confluent, forming short rows or interconnected by lower ribs forming irregular patterns, sometimes even incomplete reticulum.

SPECIMENS EXAMINED—On *Silene moorcroftiana* Wall. ex Benth.: **NEPAL, GANDAKI PRADESH, Mustang District,** Jharkot–Khinga–Yekle Bhatti–Jomsom–Syang–Marpha, 28°45′17″–49′01″N 83°41′28″–51′02″E, alt. 3100 m, 21 August 1994, leg. S. Noshiro & al., 1994 Expedition by the Society of Himalayan Botany, Tokyo, no. 9470526 (E 232984); Jomsom–Ekle Bhatti–Khingar–Jharkot, 28°47′09″–49′38″N 83°42′5″–51′07″E, alt. 3040 m, 22 September 1995, leg. M. Mikage & al., 1995 Expedition by the Herbal Garden, Kanazawa Univ., Japan, no. 9552385 (E 232977).

DISTRIBUTION—On *Caryophyllaceae: Silene moorcroftiana,* the Himalayas (India (Ladakh) and Nepal).

COMMENTS—The morphological features given in the protologue of *M. bardanense* (Chlebicki & Suková 2005) are similar to those reported here.

Silene moorcroftiana is distributed in Afghanistan, NW Pakistan, India (Jammu and Kashmir, Himachal Pradesh, and Uttar Pradesh), Nepal, and China (Tibet) (Zhou & al. 2001, Rajbhandari & Suzuki 2008, India

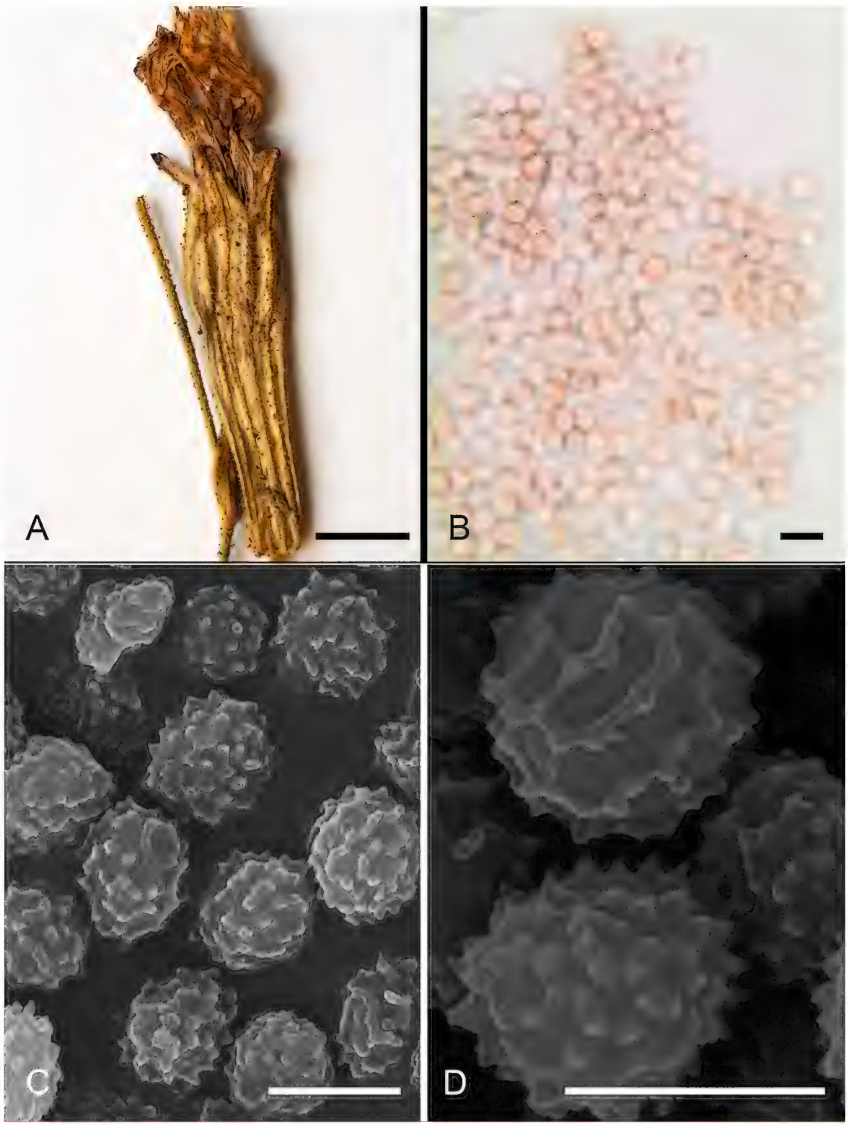

Fig. 1. *Microbotryum bardanense* on *Silene moorcroftiana* (E 232984): A. Habit; B. Spores in LM; C, D. Spores in SEM. Scale bars: A = 0.5 cm; B = 10 µm; C, D = 5 µm.

Biodiversity Portal 2020). Until now, *Microbotryum bardanense* was known only from its type locality: India, Ladakh, 20 km S of Padum, near Bardan

Monastery, alt. 3888 m (Chlebicki & Suková 2005). In the protologue, the geographic coordinates of the type locality appear to be wrong. *Microbotryum bardanense* is reported here for the first time from Nepal.

Microbotryum polygoni-alati (Thirum. & Pavgi) Vánky,
Mycotaxon 67: 49, 1998 FIG. 2

SORI in inflorescence (destroying single or groups of flowers, forming irregular bodies), in some leaves (forming irregular bodies), or on stem (forming irregular or reniform bodies); 2–10 mm long, covered by a yellow-brown peridium that ruptures irregularly, exposing a semi-agglutinated to powdery, sepia (based on Rayner 1970) or date brown (based on the Colour identification chart of Anonymous 1969) spore mass. SPORES subglobose, globose, broadly ellipsoidal, slightly irregular, ellipsoidal or ovoid, 9–12.5(–14) × (8.0–)8.5–11(–12) µm (10.9 ± 0.9 × 9.6 ± 0.6 µm) (n = 100), light to medium purplish brown; wall reticulate, 1.0–1.4 µm thick, including 0.4–0.6(–0.7) µm high muri. In SEM, spore wall reticulate, often incompletely reticulate, often with warts, mainly in the common points of the meshes; the interspaces often perforate with up to 3(–5) holes per interspace, sometimes with 1(–2) warts. Immature spores abundant, hyaline to light purplish brown, smaller than the mature spores.

SPECIMEN EXAMINED—On *Persicaria nepalensis* (Meisn.) Miyabe: **NEPAL, PROVINCE No. 1, Khumbu Region,** Rolwaling, trekking to Sagarmatha National Park, Lukla (alt. 2760 m) to Phakding (alt. 2610 m) ca 5 km, 27°41′44″N 86°44′19″E, 14 October 2002, leg. C.S. Chang & al., no. NE020610 (SNUA 61760; host plant as "*Koenigia nepalensis* D. Don", rev. S.P. Hong).

DISTRIBUTION—On *Polygonaceae: Persicaria nepalensis* [≡ *Polygonum nepalense* Meisn.; = *P. alatum* Buch.-Ham. ex D. Don]; Asia (India, Nepal, China), East Africa (Ethiopia).

COMMENTS—The morphological features of the examined specimen are similar to those reported by Vánky (2011). *Microbotryum polygoni-alati* has very characteristic spore wall ornamentation (visible particularly well in SEM) – a reticulum with interspaces, which are often perforate with ≤3(–5) holes, sometimes, with 1(–2) warts. This species is also one of the few members of *Microbotryum* that can develop sori in different organs of their hosts.

Persicaria nepalensis is distributed in East, South, and Southeast Asia, New Guinea, and Tropical Africa (Li & al. 2003) but this species has been introduced in many other regions of the world. *Microbotryum polygoni-alati* was known only from India (Thirumalachar & Pavgi 1968; Vánky 2007), China (Sichuan,

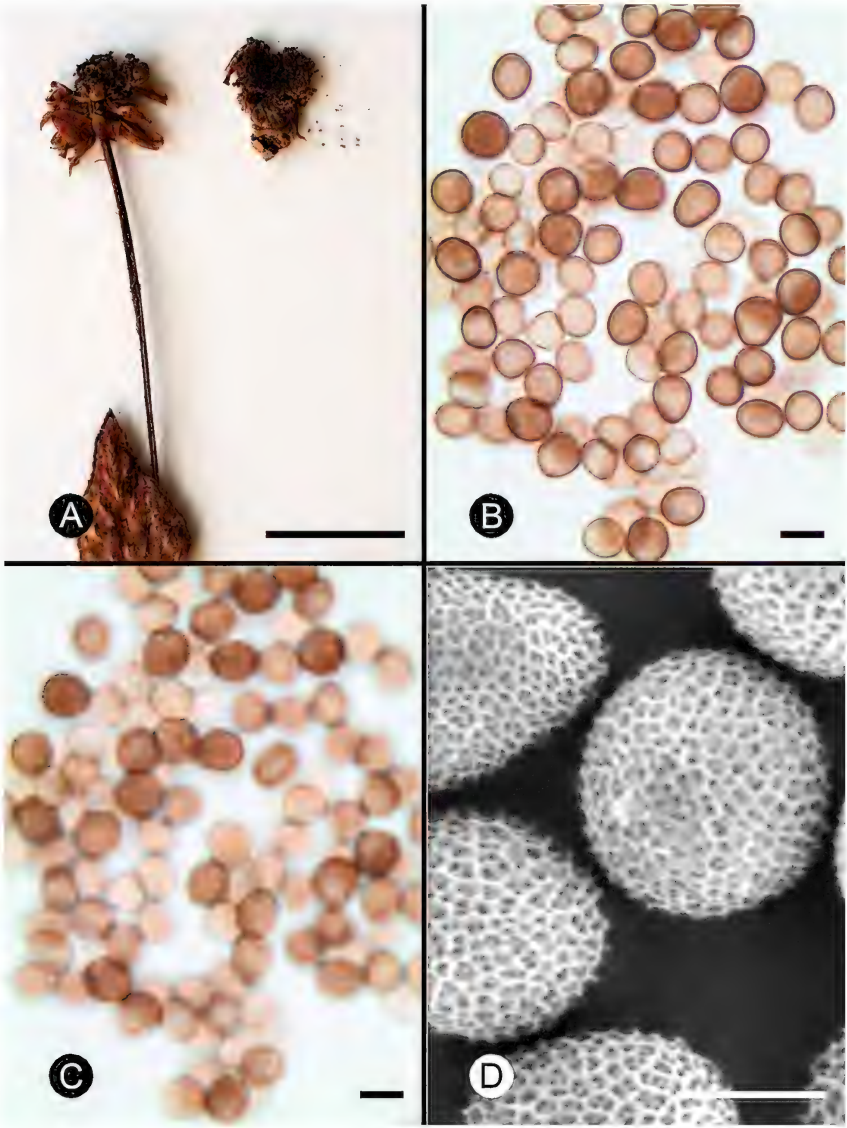

Fig. 2. *Microbotryum polygoni-alati* on *Persicaria nepalensis* (SNUA 61760): A. Habit; B. Spores in LM, median view; C. Spores in LM, surface view; D. Spores in SEM. Scale bars: A = 0.5 cm; B, C = 10 μm; D = 5 μm.

Guo 1993; Yunnan, Kakishima & al. 2000), and Ethiopia (Denchev & Denchev 2017). It is reported here for the first time from Nepal.

Acknowledgements

The visit in the herbarium of the Royal Botanic Garden Edinburgh was supported from the SYNTHESYS Project http://www.synthesys.info/ (Grant no. GB-TAF-709) financed by the European Community Research Infrastructure Action under the FP7 Integrating Activities Programme. The visit in T.B. Lee Herbarium in College of Agriculture and Life Sciences, Seoul National University was supported by the Korea Research Foundation and the Korean Federation of Science and Technology Societies Grant funded by Korea Government (MOEHRD, Basic Research Promotion Fund). The authors would also like to acknowledge Prof. Makoto Kakishima (University of Tsukuba, Tsukuba, Japan) and Dr. Shuang-Hui He (Institute of Microbiology, Beijing Forestry University, China) for critically reading the manuscript and serving as pre-submission reviewers, and Directors and Curators of E and SNUA for granting access to the collections.

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Chlorophyllum hortense newly recorded, and *C. molybdites* confirmed, from Pakistan

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Abstract—During a field survey of macrofungi from Kasur and Narowal districts, Punjab, Pakistan, some collections were found morphologically similar to species of *Chlorophyllum*. Their morphological and molecular analyses revealed two species, *Chlorophyllum hortense* (a new record from Pakistan) and *C. molybdites* (confirming a previous Pakistani record that lacked phylogenetic and detailed micro-morphological analyses).

Key words—*Agaricaceae*, agaricoid, ITS, taxonomy

Introduction

Chlorophyllum Massee is a relatively small genus in the *Agaricaceae* (Vellinga 2004b, Vellinga & al. 2011, Ge & Yang 2006). Species within this genus are saprobic, distributed in tropical to temperate regions of the world, and often found growing in urban and rural habitats (Vellinga 2004a). The genus varies from agaricoid, secotioid to gasteroid in habit. Agaricoid species are characterized by a hymenodermal pileus covering, smooth stipe, and basidiospores that either lack a germ pore or have a germ pore caused by a depression in the episporium without a hyaline covering, and a white, green, brownish or brown spore print (Vellinga 2003a, 2004b; Vellinga & al. 2011, Ge & Yang 2006, Crous & al. 2015, Loizides & al. 2020).

Chlorophyllum was previously recorded from Pakistan by Razaq & Shahzad (2012), who provided descriptions and illustrations of *C. molybdites* and *C. rhacodes* [as *Macrolepiota rachodes*], but without phylogenetic analyses and more detailed descriptions these cannot be accepted as authenticated identifications. Our research focuses on the identification of *Chlorophyllum* specimens collected in Kasur and Narowal districts of Punjab, Pakistan. The identification of taxa is based on both morphological characters and nrDNA ITS phylogenetic sequence analysis.

Material & methods

The samples were collected from Kasur and Narowal district, Punjab, Pakistan during monsoon of 2015 and 2019.

The Köppen–Geiger climate classification (Geiger 1954, 1961) describes the climate of Kasur district as warm semi-arid. Ground vegetation was sparse at the collection site, with patches of grass along the bank of BRB canal. Dominant tree species include *Dalbergia sissoo* DC. and *Vachellia nilotica* (L.) P.J.H. Hurter & Mabb. Köppen–Geiger (Geiger 1954, 1961) classifies the Narowal district as humid subtropical. The collection site was a grassy ground. Broad-leaved tree species including *D. sissoo* and *Eucalyptus camaldulensis* Dehnh. were observed 30–50 m away from the collection site.

The specimens were photographed at the sampling site, and the macroscopic characters were recorded in the field. Munsell (1975) was followed for color notation. The specimens were air dried for further analyses and deposited in the Herbarium of University of the Punjab, Quaid-e-Azam Campus, Lahore, Pakistan (LAH).

For microscopic studies, tissues from different parts of the basidiomata were rehydrated in KOH (2%) and mounted in Congo red (1%). Micro-morphological features were measured using calibrated Motic Images Plus 2.0 software. Genomic DNA was extracted using Extract-N-Amp™ kit following manufacturer's instructions. PCR amplification of the internal transcribed spacer region was carried out using ITS1F/ITS4 primer combination (White & al. 1990, Gardes & Bruns 1993). PCR products were purified and both strands were sequenced from Beijing Genomic Institute (BGI), P.R. China.

For phylogenetic analysis, consensus sequences were generated in BioEdit (Hall 1999) and BLAST searched at NCBI (https://www.ncbi.nlm.nih.gov/) to retrieve the sequences of closely related *Chlorophyllum* spp. from the database. Sequences mentioned in the published literature were also included from the database in final ITS matrix to represent different sections in the genus (Ge & al. 2018). *Agaricus campestris* L. was chosen as the outgroup. All the sequences were aligned online using MUSCLE (Edgar 2004). The final aligned data set was analyzed through MEGA 6.0 software for reassessing the phylogeny. Tamura 3-parameter (Tamura 1992) was selected as evolution model for maximum likelihood analysis using best-fit substitution model approach in MEGA (Tamura & al. 2013). A discrete gamma

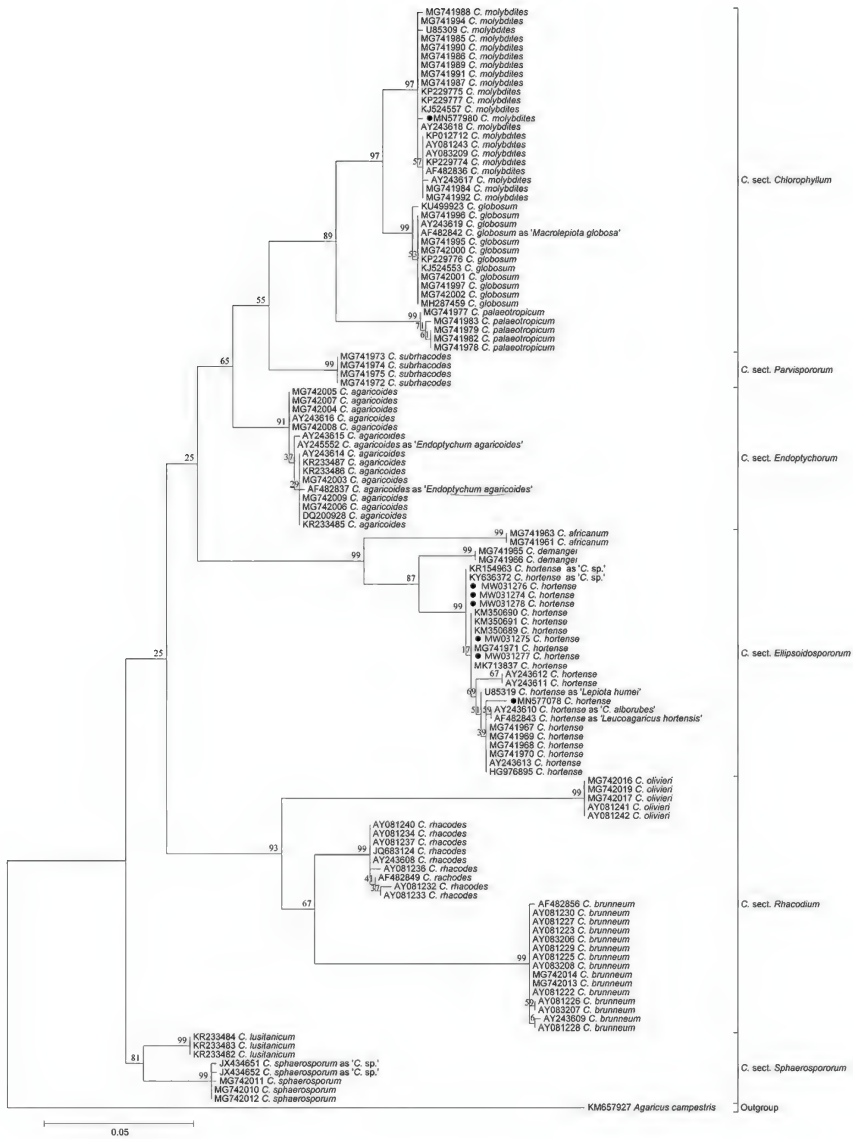

FIGURE. 1. Molecular phylogenetic analysis of ITS sequences of *Chlorophyllum* species. Section names are given on the right. The sequences generated during this study are marked with bullets.

distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.2606)).

Phylogenetic results

The ITS dataset included a total of 125 nucleotide sequences. There were a total of 726 positions in the final matrix. All positions were used in the analysis. Among these positions, 477 were conserved, 227 were variable, 183 were parsimony informative. The maximum likelihood tree is given in Figure 1. There were total six major clades representing six infrageneric groups and an outgroup. The topology of the tree is similar to the previous phylogeny reconstructed by Ge & al. (2018). The sequences from Pakistani collections clustered within *C.* sect. *Chlorophyllum* Massee (*C. molybdites*) and *C.* sect. *Ellipsoidospororum* Z.W. Ge (*C. hortense*) along with similar sequences of *Chlorophyllum* species from different parts of the world.

Taxonomy

Chlorophyllum hortense (Murrill) Vellinga, Mycotaxon 83: 416 (2002) Figs 2a–d, 3

Basidiomata agaricoid. Pileus 3–6.1 cm broad, slightly umbonate, conical to convex and flat at maturity; central disc yellowish brown (7.5YR5/8); surface dry, matt, scaly, scales furfuraceous, radially arranged, concentrated near the center and sparse towards margins; squamules present towards the margins, grayish (10Y7/2); margin slightly striate and cracked or wavy. Lamellae crowded, free, off-white (2.5Y9/2) to yellowish green (10Y9/4), with entire white edge. Lamellulae lengths variable. Stipe 9.1 × 1 cm, cylindrical; base slightly broadening ≤1.4 cm; surface longitudinally striate; striations light yellowish brown (2.5Y7/4), slightly pink (10P7/10) at the site of attachment with the pileus and around the annulus. Annulus double, superior, persistent, having pinkish tint close to the stipe. Context soft, brittle, white, becoming pinkish (10P7/10) when bruised.

Basidiospores [70/6/6] (6.8–)7.2–9.4(–10.8) × (5.3–)5.8–6.4(–6.8) µm, Q = (1.2–)1.3–1.4(–1.5), avQ = 1.3, ellipsoid with rounded apex, thick walled; germ pore absent; dextrinoid, reddish in Congo red. Basidia (24–) 24.8–31.2(–34.9) × (8.7–)9–10.3(–11.8) µm, clavate, 2–4 sterigmata, most commonly 2-sterigmate. Lamellae edge sterile. Cheilocystidia (28.6–) 35.2–58.9(–62.1) × (6.2–)7.3–9(–9.9) µm subcylindric to slightly fusiform or very narrowly clavate. Pleurocystidia absent. Pileipellis hyphae (from the background) (4.2–)6.2–9.1(–10) µm in diameter, long, cylindrical, frequently septate, branched; terminal elements clavate to narrowly clavate

FIGURE. 2. ***Chlorophyllum hortense*** basidiomata: A, B. LAH36664; C, D. LAH36661. ***Chlorophyllum molybdites*** basidioma: E, F. LAH36660. Scale bars = 1 cm. Photographs by Mughees Hamid and Humaira Bashir.

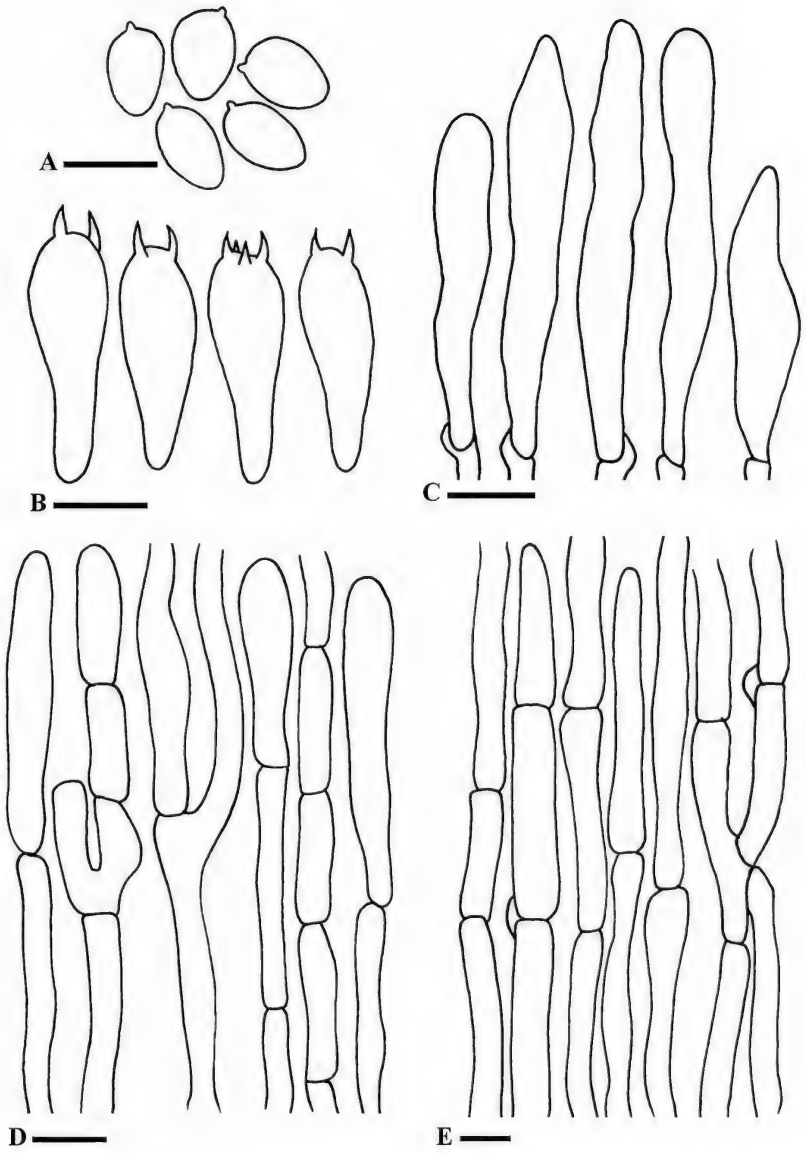

FIGURE. 3. *Chlorophyllum hortense* [LAH36661]. A. Basidiospores; B. Basidia; C. Cheilocystidia; D. Pileipellis (hyphae from the background); E. Stipitipellis. Scale bars = 10 μm. Drawing by Sana Jabeen.

forming a trichoderm, pale yellow from the disc and hyaline from the margins in KOH. Stipitipellis hyphae (7.2–)8.2–10.2(–10.4) µm wide, filamentous, branched, with narrow terminal cells, septate, clamped septa rare, hyaline in KOH.

Material examined: **PAKISTAN. Punjab, Gujranwala division**, Narowal district, Bola Bajwa, 234 m asl, on soil, 14 August 2015, Humaira Bashir RN1S53 (LAH36661; GenBank MN577078); **Lahore division**, Kasur district, near BRB Canal, 218 m asl, on soil, 30 July 2019, Mughees Hamid S#3SJ45 (LAH36662; GenBank MW031274); S#7SJ37 (LAH36663; GenBank MW031275); S#6SJ44 (LAH36664; GenBank MW031276); 1 August 2019 Mughees Hamid S#28SJ38 (LAH36665; GenBank MW031277); 9 August 2019 Mughees Hamid S#63SJ42 (LAH36666; GenBank MW031278).

Chlorophyllum molybdites (G. Mey.) Massee,
Bull. Misc. Inf., Kew 1898(138): 136 (1898) Figs 2 e,f, 4

Basidioma agaricoid. Pileus 7.6 cm in diameter, spherical when young, plane when mature; margins slightly cracked; central disc plate-like, brownish black (7.5YR3/6) to dull yellow orange (10YR6/10); surface creamy white (5Y9/4), minutely pubescent with distinct brown fibrils and patches of squamules; squamules uplifted, dull yellow orange (10YR6/10), concentrated near the center. Lamellae free, crowded, regular, even, light green (5GY8/4), edges entire. Lamellulae three tiered. Stipe 6.3 × 0.8 cm, cylindrical, straight to bent, slightly bulbous at the base, light brown (10YR5/6) to dark brown (10YR3/6), central to the pileus; surface smooth, dry, glabrous. Annulus double edged, edges ruptured, persistent, fixed, central to the stipe, upper surface white, lower surface brown. Context slightly tough, and hard particularly of stipe, white, becoming pinkish (10P7/10) when bruised.

Basidiospores [20/1/1] (8.6–)9.3–12.2(–12.5) × (6–)6.6–7.7(–7.8) µm, Q = (1.2–)1.3–1.5(–1.6), avQ = 1.3, ellipsoid to amygdaliform, smooth, with truncate apex and visible germ pore and prominent apiculus, thick-walled, dextrinoid, pinkish in Congo red, light green in 5% KOH. Basidia (22.8–)24–28.6(–29.6) × (10.1–)10.6–13.5(–14) µm, clavate, 2–4 sterigmate, thin-walled. Lamella edge sterile. Cheilocystidia (20–)24.3–28.8(–31.1) × (7.6–)8.3–10.2(–11.7) µm, clavate to broadly clavate or sphaeropedunculate, hyaline to yellowish in KOH. Pleurocystidia absent. Pileipellis (hyphae from the background) trichoderm, hyphae forming a palisade of cells (7.6–)10.1–14(–14.7) µm in diameter, apical cells narrowly clavate and slightly long, pale yellow to brownish from the central disc and hyaline from the margins in 5% KOH. Stipitipellis hyphae (3.5–)4.9–8.3(–8.8) µm wide, filamentous, branched, frequently septate, clamped septa rare, broad terminals, hyaline in KOH.

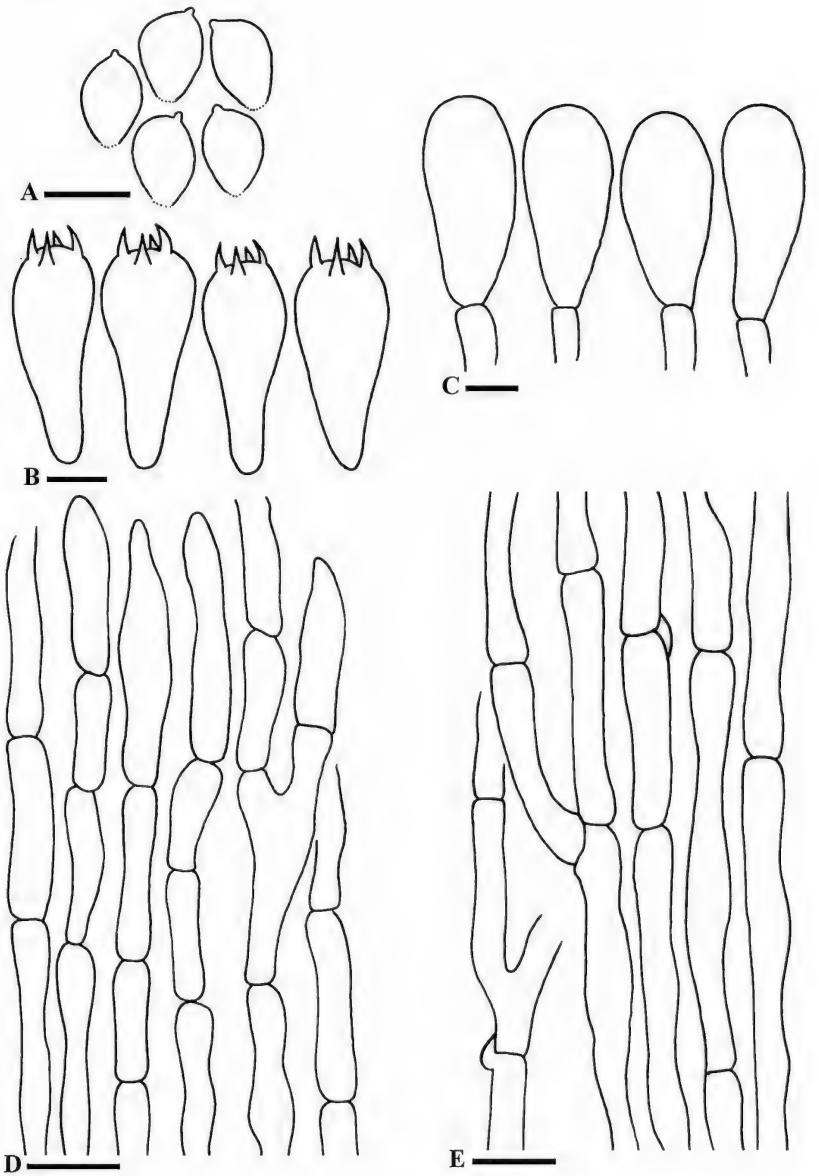

Figure. 4. *Chlorophyllum molybdites* [LAH36660]. A. Basidiospores; B. Basidia; C. Cheilocystidia; D. Pileipellis (hyphae from the background); E. Stipitipellis. Scale bars: A–C = 10 µm; D, E = 20 µm. Drawing by Sana Jabeen.

Material examined: **PAKISTAN. Punjab, Gujranwala division,** Narowal district, Bola Bajwa, 234 m asl, on soil, 14 August 2015, Humaira Bashir RN2 (LAH36660; GenBank MN577080).

Discussion

Two *Chlorophyllum* species from Kasur and Narowal district, Punjab, Pakistan have been identified. Both species have brown scales on the cap, which differ slightly in shape, but the main differences are in the color of the lamellae, spores, basidia, and cheilocystidia.

Chlorophyllum hortense was previously known under different species names in multiple genera including *Lepiota* (Pers.) Gray, *Leucoagaricus* Locq. ex Singer, and *Macrolepiota* Singer, until Vellinga (2003a) used molecular data and placed the taxon in *Chlorophyllum*. It is placed in *C.* sect. *Ellipsoidospororum,* characterized by slender basidiomata having furfuraceous squamules on the pileus, ellipsoid basidiospores without a germ pore, and subcylindric to slightly fusiform cheilocystidia (Ge & al. 2018). This species can be separated from other taxa in *C.* sect. *Ellipsoidospororum* by its white basidiomata, ellipsoid basidiospores with a rounded apex and lack of a germ pore, frequent 2-spored basidia, and subcylindric to fusiform cheilocystidia (Ge & al. 2018). It should be noted that although 2-spored basidia are rare in the *Agaricaceae,* we have frequently observed 2-spored basidia both previously and during this investigation. These specimens showed remarkable similarity with previous descriptions of the species by several workers from different parts of the world (Murrill 1914, Pegler 1983, Aberdeen 1992, Akers & Sundberg 1997, Vellinga 2003a, Ge & Yang 2006, Nascimento & Alves 2014, Alves & al. 2016). Clamp connections were also observed in the stipitipellis of Pakistani collections. Distinct clamp connections were reported by Akers & Sundberg (1997) and Vellinga (2003a), but not observed by Pegler (1983) and Ge & Yang (2006).

Chlorophyllum hortense is widely distributed and known (under various names) from Africa, Asia, Australia, and North and South America (Murrill 1914, Dennis 1952, Aberdeen 1962, 1992; Smith 1966; Heinemann 1973; Pegler 1983, 1997; Franco 1994; Akers & Sundberg 1997; Vrinda & al. 1999; Hemmes & Desjardin 2002; Vellinga 2003a; Sobestiansky 2005; Ge & Yang 2006; Gimenes 2007; Farook & al. 2013; Nascimento & Alves 2014; Alves & al. 2016).

Chlorophyllum molybdites [= *C. esculentum* Massee, the generic type] is characterized by olive to greenish-white basidiospores with a truncate apex, broadly clavate to sphaeropedunculate cheilocystidia, and a palisade-like

pileus covering of hyphae with terminal clavate to subfusiform elements (Ge & al. 2018). The specimen identified as *C. molybdites* during this investigation showed similar characters as described by Pegler (1983), De Meijer & al. (2007), Alves & al. (2016, 2019), and Bijeesh & al. (2017). It is characterized by the green lamellae and green basidiospores (>10 µm) with a truncate apex and a prominent germ pore (Ge & al. 2018, Alves & al. 2019). This species is considered toxic and causes gastrointestinal distress; the symptoms can be quite serious. The toxicity of this species may depend upon climatic conditions, habitat alone, and the susceptibility of the individual (Graff 1927, Pegler 1983, Reid & Eicker 1991, Lehmann & Khazan 1992; Benjamin 1995). This species has been reported worldwide (Reid & Eicker 1991).

Chlorophyllum molybdites has been reported previously in the cold desert climate of Gilgit-Baltistan, Pakistan (Razaq & Shahzad 2012). Photographs by Razaq & Shahzad (2012) show a specimen with persistent scales that are grayish rather than dark brown and the lamellae appear white, which also differs from previous descriptions of *C. molybdites*. Since Razaq & Shahzad's (2012) identification was based solely on macroscopic characters without detailed anatomical observations and lacking a herbarium specimen and phylogenetic analyses, their Pakistan report of *C. molybdites* cannot be authenticated.

Chlorophyllum rhacodes (Vittad.) Vellinga [≡ *Macrolepiota rhacodes* (Vittad.) Singer] has also been reported from Pakistan (Razaq & Shahzad 2012, as *Macrolepiota*). *Chlorophyllum rhacodes* can be identified by large basidiomata with darker pileus scales and a bulbous stipe with a double crowned annulus. Anatomically this species can be distinguished from other *Chlorophyllum* species by its large, broad (10–35 × 8.5–25 µm) sphaeropedunculate cheilocystidia. Its basidiospores are 8.8–12.7 × 5.4–7.9 µm with a rounded to truncate apex and visible germ pore, and its pileipellis is a tightly packed hymeniderm of cylindrical and flexuous, or narrowly clavate or narrowly lageniform elements (Vellinga 2003b). The Pakistani collection identified as *Macrolepiota rhacodes* by Razaq & Shahzad (2012) shared some features with the type specimen, including the larger basidiomata with dark brown scales, double crowned annulus, a stipe with bulbous base; and the spore shape and size (Razaq & Shahzad 2012). We can conclude that *M. rhacodes* described by Razaq & Shahzad (2012) probably represents *C. rhacodes*; but again, without an herbarium specimen, we cannot obtain the detailed description and molecular phylogeny necessary to authenticate this record.

This investigation reports *C. hortense* as a new record from Pakistan and confirms the occurrence of *C. molybdites* from Pakistan, based on detailed morphological descriptions and molecular phylogenetic evidence. Occurrence of *Chlorophyllum* species in Pakistan considerably extends their known distribution into warm semi-arid and humid subtropical regions.

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New record of *Geopora sumneriana* from Pakistan

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Abstract—A new record of *Geopora sumneriana* is presented from Pakistan. Specimens were collected under *Cedrus deodara* trees in Chitral district of Khyber Pakhtunkhwa province during 2018. The newly reported specimens are illustrated and described using morphological characters and phylogenetic analysis of the internal transcribed spacer region (ITS).

Key words—cup fungi, *Pezizales*, phylogeny, *Pyronemataceae*, taxonomy

Introduction

Geopora Harkn. (*Pyronemataceae*, *Pezizales*) was established by Harkness (1885) based on the hypogeous type species *Geopora cooperi* Harkn. With the addition of semihypogeous and epigeous species, the genus has since been expanded to 27 species and six infraspecific taxa (Index Fungorum 2020). Five species—*G. arenosa* (Fuckel) S. Ahmad, *G. foliacea* (Schaeff.) S. Ahmad, *G. arenicola* (Lév.) Kers, *G. cooperi,* and *G. ahmadii* Saba & al.—have been reported from Pakistan (Ashraf & Khalid 2012, Saba & al. 2019).

Geopora taxa are morphologically characterized by ascomata that are partially or completely subterranean and covered with flexible, thin or thick, septate excipular hairs; a whitish, greyish or yellowish grey hymenium; an excipulum divided into two (the ectal and medullary) layers; operculate cylindrical asci; uniseriate, ellipsoid or ellipsoidal-

fusiform, predominantly smooth (although *G. lateritia* (Fogel & States) Healy & M.E. Sm. has ornamented spores; Grupe & al. 2019) ascospores with one or two guttules (Tamm & al. 2010, Perić & Perić 2011). *Geopora* species fruit on soil, sand, or often rotten and decaying plant materials and form ectomycorrhizal relationships with trees (Tamm & al. 2010).

Tamm & al. (2010) concluded that previously used taxonomic characters —such as ascospore size, hymenial color, ectomycorrhizal relationships, ascomatal shape and position, and ploidy level—are insufficient for circumscribing *Geopora* species. Similarly, geographic research data also do not help in delimiting species within the genus. An integrative approach to taxonomy combining morphological and DNA sequence data—as applied in many other groups of fungi (e.g., Ko & al. 2011, Stefani & al. 2014, Ali & al. 2016, Skrede & al. 2017, Sousa & al. 2017, Haelewaters & al. 2018, Song & al. 2019)—has been suggested for classifying species within *Geopora* (Tamm & al. 2010, Flores-Rentería & al. 2014). The description of *G. ahmadii,* for example, was supported by both morphological and molecular phylogenetic data (Saba & al. 2019).

During our macrofungal field surveys, we collected some gregarious specimens of *Geopora* on moist soil under *Cedrus deodara* (Roxb. ex D. Don) G. Don trees in Chitral District, Northern Pakistan. Our preliminary field observations, morphological examinations, and ITS sequence data identified the specimens as *G. sumneriana,* which constitutes the first report of this species in Pakistan.

Materials & methods

Microscopic study

The specimens collected in the Chitral district were dried in a food dehydrator at 40 °C for 8 hours. Microscopic characters were measured and photographed using a Leitz light microscope and Leica camera. Fungal tissues were mounted in water, KOH, and Congo red. The specimens were deposited in the herbarium of Plant Sciences Department, Quaid-i-Azam University, Islamabad, Pakistan (ISL).

DNA extraction, PCR amplification, DNA sequencing

DNA was extracted from a small section of the dried apothecium using a modified CTAB protocol (O'Donnell & al. 2009). The internal transcribed spacer region (ITS) was amplified with the primer pair ITS1F and ITS4 (White & al. 1990, Gardes & Bruns 1993). PCR parameters were set as follows: initial denaturation at 95 °C for 5 min, followed by 38 cycles of denaturation at 95 °C for 30 s, annealing at 56 °C for 40 s, and extension at 72 °C for 1:30 min; and a final extension at 72 °C for 10 min. The PCR product was purified using the Thermo Scientific™ GeneJET PCR

Table 1. Geopora species and outgroup species used in the phylogenetic analyses. The newly generated sequence is presented in bold font.

TAXA	COUNTRY	VOUCHER/ ISOLATE/STRAIN	ITS	REFERENCES
Geopora ahmadii	Pakistan	MSM0091	KY805995	Saba & al. 2019
	Pakistan	MSM00163	KY805996	Saba & al. 2019
G. arenicola	Finland	H SJ-4366	FM206457	Tamm & al. 2010
	Finland	TAA 188638	FM206453	Tamm & al. 2010
	Finland	H VH23012	FM206454	Tamm & al. 2010
	Finland	H VH22603	FM206455	Tamm & al. 2010
	Estonia	TAAM 192325	FM206456	Tamm & al. 2010
G. cervina	Estonia	TAA 188304	FM206417	Tamm & al. 2010
	Estonia	TAA 117898	FM206419	Tamm & al. 2010
	Estonia	TAA 188517	FM206418	Tamm & al. 2010
G. cercocarpi	USA	Kropp2	HQ283097	Southworth & Frank 2011
	USA	Kropp1	HQ283096	Southworth & Frank 2011
	USA	SOC1596	HQ283094	Southworth & al. 2011
G. clausa	USA	OSC 58245	MK359192	Grupe & al. 2019
G. cooperi	Spain	101GA	AF387651	Gutierrez & al. (unpubl.)
	Spain	108GC	AF387649	Gutierrez & al. (unpubl.)
	Spain	109GC	AF387650	Gutierrez & al. (unpubl.)
G. foliacea	Finland	H RS-34685	FM206428	Tamm & al. 2010
	Finland	H RS-29584	FM206424	Tamm & al. 2010
G. gilkeyae	USA, CA	src515	DQ974731	Smith & al. 2007
G. pinyonensis	USA, AR	DGB 27586	KF768652	Flores-Rentería & al. 2014
	USA, AR	DGB 27586	KF768653	Flores-Rentería & al. 2014
G. sepulta	Estonia	TAA 192333	FM206431	Tamm & al. 2010
	Estonia	TAA 192311	FM206432	Tamm & al. 2010
G. sumneriana	**Pakistan**	**ISL99125**	**MN860070**	**This paper**
	India	RS-18-1000	MN200944	Sharma (unpubl.)
	Italy	16978	JF908024	Osmundson & al. 2013
G. tenuis	Finland	H RS-09584	FM206402	Tamm & al. 2010
	Estonia	TAA 188326	FM206397	Tamm & al. 2010
	Estonia	TAA 188331	FM206396	Tamm & al. 2010
G. tolucana	USA	375	MK842019	Shemesh & al. (unpubl.)
	USA	217	MK841861	Shemesh & al. (unpubl.)
	USA	376	MK842020	Shemesh & al. (unpubl.)
	USA	222	MK841866	Shemesh & al. (unpubl.)
	USA	215	MK841859	Shemesh & al. (unpubl.)
Trichophaea hybrida	Estonia	TAA 192334	FM206477	Tamm & al. 2010
Tarzetta catinus	Estonia	TAA 192291	FM206478	Tamm & al. 2010

purification kit according to the manufacturer's instructions and commercially sequenced by Macrogen (Korea).

Phylogenetic analysis

The raw sequence reads were manually assembled, checked, and corrected in CLC Main Workbench version 8.1 (QIAGEN Aarhus A/S). The ITS sequence dataset included 37 sequences, including 34 *Geopora* sequences downloaded from NCBI GenBank, one sequence generated during the present study, and two outgroup sequences (*Tarzetta catinus* (Holmsk.) Korf & J.K. Rogers and *Trichophaea hybrida* (Sowerby) T. Schumach.) also downloaded from GenBank (Table 1). The ITS dataset was aligned using the Muscle E multiple alignment tool in MEGA v. 7.0 (Kumar & al. 2016). Gaps and missing data were excluded from the dataset.

The best-fit nucleotide substitution model was chosen from the model test tool in MEGA 7.0 (Kumar & al. 2016) using the Akaike Information Criterion (AIC). The phylogeny of the ITS sequences was constructed using maximum likelihood inference (ML) under the General Time Reversible Model of nucleotide substitution (GTR + I + Γ; Nei & Kumar 2000). Bootstrap support values were obtained from 1000 replications. A heuristic search was performed on the matrix of pairwise distances using maximum composite likelihood method of estimation and Neighbor-Joining and BioNJ algorithms. MEGA 7.0 (Kumar & al. 2016) was used for the phylogenetic analysis. The final tree was visualized and formatted in FigTree v.1.4.4 and TreeGraph 2.0 (Fig. 1).

Bayesian inference with Metropolis-coupled Markov Chain Monte Carlo (MCMC) method was used to estimate posterior probabilities in MrBayes version 3.2.7a (Ronquist & al. 2012). The nucleotide substitution model selected was GTR + I + Γ. The analysis was carried out in two runs and four chains, each with 1,000,0000 generations. The temperature (1.0) was used for the cold chain. The MCMC model parameters were adjusted to every 500 generations and trees were sampled every 1000 generations. A default burn-in of 25% was used by MrBayes to discard samples from the cold chain and 3020 trees were summarized to construct a consensus tree. Bayesian posterior probability values of >0.8 were used in the final fit-tree.

Phylogenetic results

Our query sequence Blast produced the highest hits for *Geopora sumneriana* from Italy (JF908024, 99.82 identity) and *G. sumneriana* from India (MN200944,

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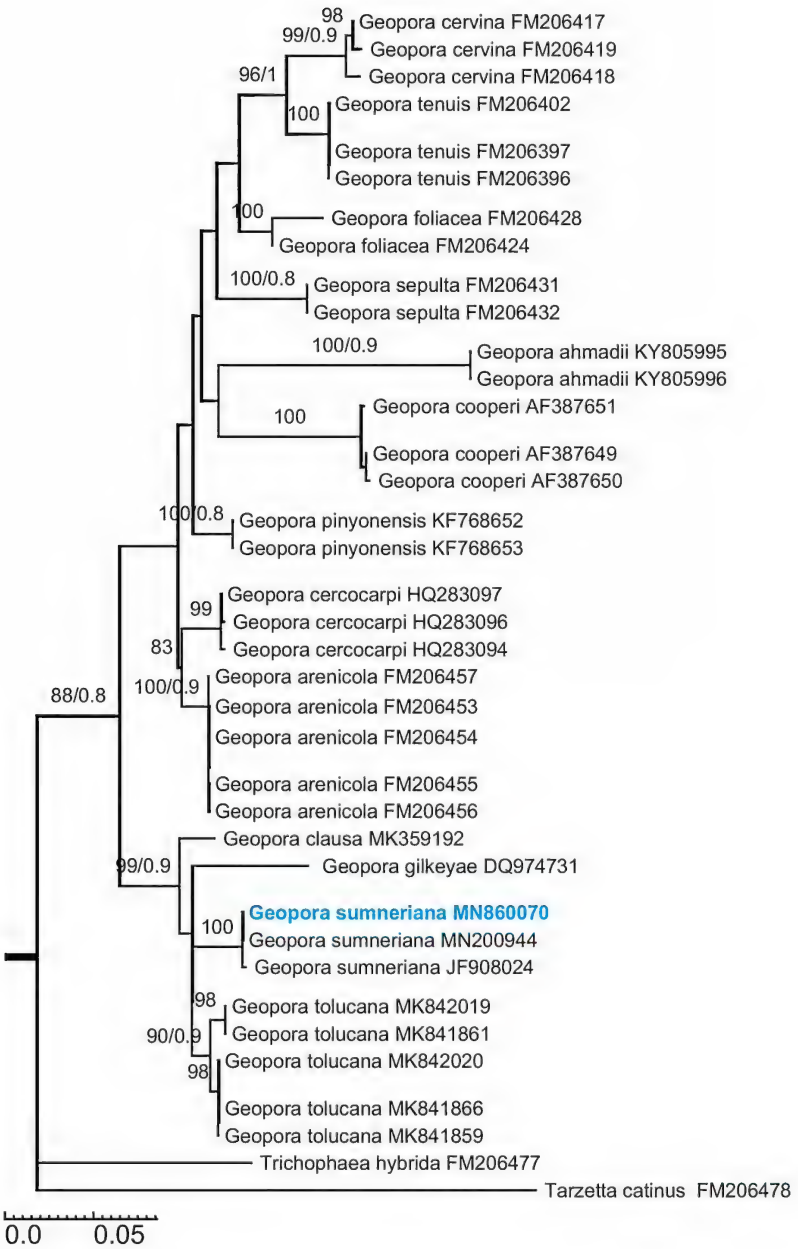
Figure 1. A phylogram of *Geopora* species constructed from ITS sequences. Maximum likelihood (ML) and Bayesian inference (BI) methods of phylogeny were conducted in MEGA 7.0 and MrBayes 3.2.7a. Bootstrap probability values >80% and posterior probability values ≥0.80 are shown above the branches. *Geopora sumneriana,* investigated in this paper, stands in blue font. *Tarzetta catinus* and *Trichophaea hybrida* represent outgroup taxa.


98
Geopora cervina FM206417
99/0.9
Geopora cervina FM206419
Geopora cervina FM206418
96/1
100
Geopora tenuis FM206402
Geopora tenuis FM206397
Geopora tenuis FM206396
100
Geopora foliacea FM206428
Geopora foliacea FM206424
100/0.8
Geopora sepulta FM206431
Geopora sepulta FM206432
100/0.9
Geopora ahmadii KY805995
Geopora ahmadii KY805996
100
Geopora cooperi AF387651
Geopora cooperi AF387649
Geopora cooperi AF387650
100/0.8
Geopora pinyonensis KF768652
Geopora pinyonensis KF768653
99
Geopora cercocarpi HQ283097
Geopora cercocarpi HQ283096
83
Geopora cercocarpi HQ283094
88/0.8
100/0.9
Geopora arenicola FM206457
Geopora arenicola FM206453
Geopora arenicola FM206454
Geopora arenicola FM206455
Geopora arenicola FM206456
Geopora clausa MK359192
99/0.9
Geopora gilkeyae DQ974731
Geopora sumneriana MN860070
100
Geopora sumneriana MN200944
Geopora sumneriana JF908024
98
Geopora tolucana MK842019
90/0.9
Geopora tolucana MK841861
98
Geopora tolucana MK842020
Geopora tolucana MK841866
Geopora tolucana MK841859
Trichophaea hybrida FM206477
Tarzetta catinus FM206478
0.0
0.05

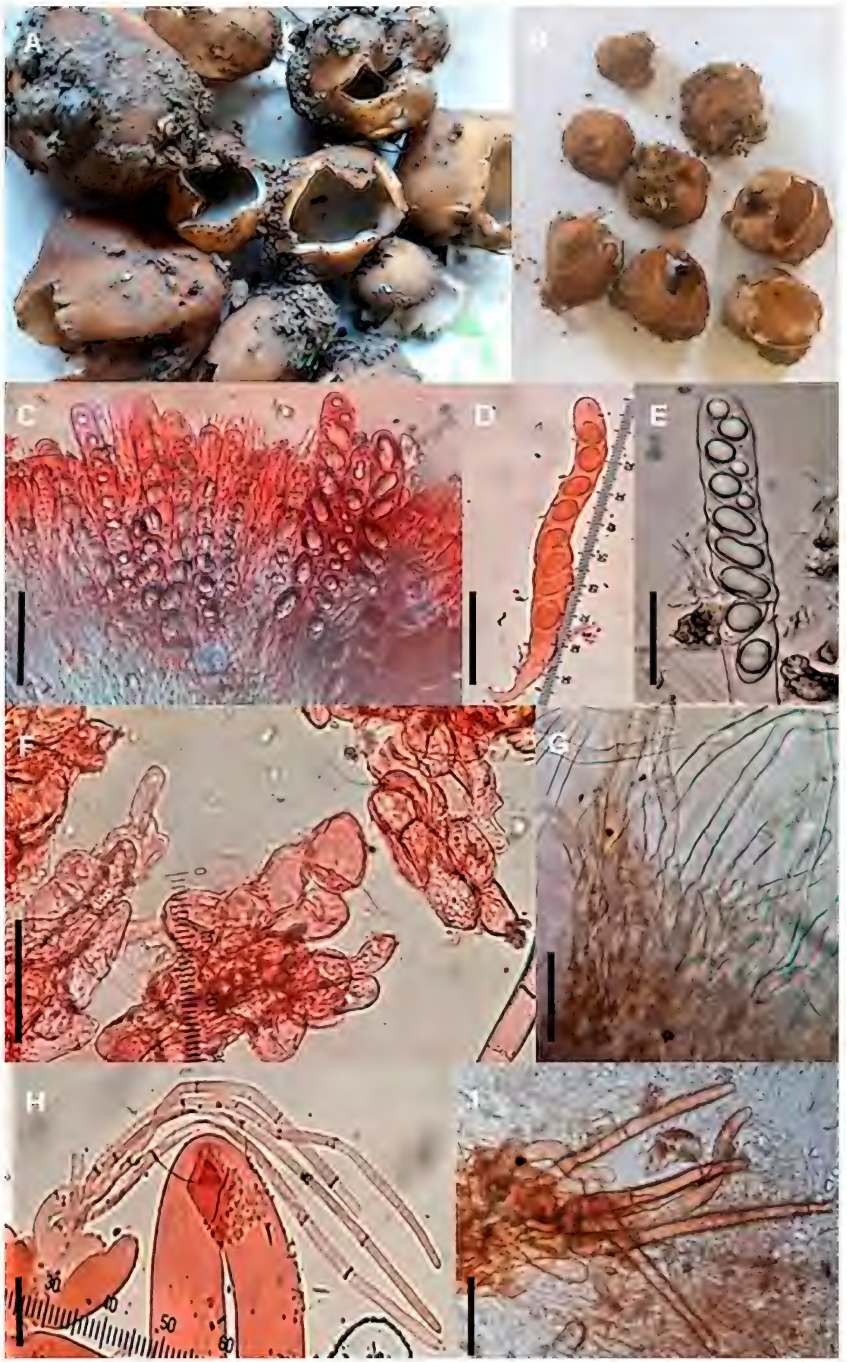
100 identity). *Tarzetta catinus* and *Trichophaea hybrida* were chosen for rooting purpose due to their close phylogenetic relationship with *Geopora* species (Perry & al. 2007, Saba & al. 2019). The best tree recovered from ML analysis (–lnL = 1925.2196) is shown in Fig. 1. Our *G. sumneriana* ITS sequence clusters with the *G. sumneriana* sequences from Italy and India (Fig. 1) in a clade with 100% ML bootstrap support; however, Bayesian inference support was only moderate (posterior probability = 0.65).

Taxonomy

Geopora sumneriana (Cooke ex W. Phillips) M. Torre,
Anales Inst. Bot. Cavanilles 32(2): 96. 1976 ["1975"]. Plates 1, 2

Apothecium large, sessile, outer surface brown or deep brown, covered with fine hairs and dust particles, scaly, rough, brittle, at first subterranean and globular in shape, closed, upon maturity a small opening arising at the top with regular margins, later breaking through soil, then margins splitting into 4–6 lobes or rays, resembling star or crown-shape, then making a wide bowl shape; at maturity semihypogeous or partially immersed in the soil; stem absent, apothecium attached to the substrate through a tiny tubular structure in the center or brown mycelium. Hymenium deeply concave, smooth, whitish and at maturity creamy or pale beige color. Ascus hyaline, eight-spored, operculate, cylindrical, 182–300 × 16–27 µm, rounded at the top (16–27 µm diam.), narrower at the base (6–8 µm diam.). Ascospores ellipsoid and fusiform, uniseriate, sometimes containing two larger oil drops and many small oil drops around them, or mostly one oil drop, 28–33 × 12.9–15 µm, hyaline, smooth, thick walled, colorless in water, in Melzer's reagent no change in color observed. Paraphyses thread-like and narrow, cylindrical, hyaline, broader at the middle ≤3–4 µm diam., slightly enlarged at the top ≤4–6 µm diam., septate. Ectal Excipulum is textura globuloso-angularis, made up of oval or irregular shaped cells, 17.5–42.5 × 10–28 µm, transparent or brown at the surface. Hairs arising from ectal excipulum, septate, lighter or darker brown, thick-walled, blunt ends and rounded, very long, 12–15 µm diam., cytoplasm with numerous crystals. Anchor Hyphae septate, dense, very long, light brownish and curled with rounded ends.

Plate 1. *Geopora sumneriana* (ISL99125): A, B. Maturing and immature apothecia; C. Asci and paraphyses; D. Ascus; E. Ascus with ascospores, some ascospores with only one large oil drop and others with two oil drops, one large and one small; F. Ectal excipulum cells; G. Hyphae; H. Septate paraphyses; I. Excipular hairs with base. Scale bars: C = 200 µm; F = 50 µm; G–I = 20 µm.


A
B
C
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E
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I
30
40
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60

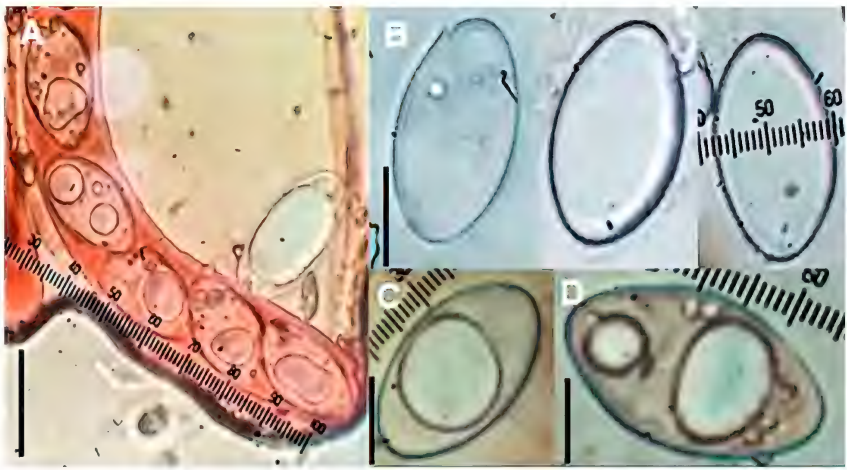

Plate 2. *Geopora sumneriana* (ISL99125): A. Part of ascus showing ascospores with guttules; B. Ascospores without guttules, showing the ellipsofusoid shape; C. Ascospore with one guttule; D. Ascospore with two guttules. Scale bars: A = 200 µm; B–D = 20 µm.

Habitat In small groups, on moist ground beneath cedar (*Cedrus deodara*) and among the rotten cedar needles.

Material examined—**PAKISTAN, Khyber Pakhtunkhwa Province, Chitral,** Booni Gol Qasumandeh, collected beneath *Cedrus deodara*, alt. 2159 m a.s.l., 19 April 2018, leg. I. Maqsad (ISL99125; GenBank MN860070).

Discussion

In the present study, we discovered that our specimens closely match the original and subsequently published descriptions and illustrations of *Geopora sumneriana* (and its synonyms), a species widely known from Europe (Phillips 1887, Berkeley & Broome 1866, Yao & Spooner 1996, Perić & Perić 2011). The identification of our material as *G. sumneriana* is supported by BLAST matches with *G. sumneriana* sequences from India and Italy and our phylogenetic analysis (Fig. 1). This represents the first report of *G. sumneriana* from Pakistan.

The distinguishing characters of *G. sumneriana* include relatively large apothecia and asci, ellipsoid and fusiform ascospores (usually with two oil drops) measuring (26.7–)28.7–31.6(–32.1) × (13.2–)14.7–16.0(–16.3) µm (Torre 1975), and a habit under coniferous trees in spring (Phillips 1887, Perić & Perić 2011).

However, we did observe one difference in the morphological characters of our Pakistani material. Perić & Perić (2011) mention that the ascospores of *G. sumneriana* generally contain two oil drops but rarely one, whereas we observed generally one, rarely two oil drops in our specimens, potentially due to differences in developmental stage; our specimens appeared to be relatively young to immature (Plate 2).

Geopora sumneriana and *G. arenosa* possess a similar ascospore spore size and shape; however, *G. arenosa* can be distinguished by its smaller apothecia (c. 15 mm diam. in *G. arenosa* vs. >30 mm diam), its phenology (late summer to autumn), and association with pine; Yao & Spooner 1996, 2003) instead of cedar. Also, the ascospore size and shape of our specimen was larger than in *G. arenosa* (25–29 × 12.5 µm; Yao & Spooner 2003). As no sequence data have been obtained from *G. arenosa*; efforts to re-collect and sequence specimens of this species would help elucidate its placement among related *Geopora* species.

The morphological species concept in *Geopora*, as in many other fungal groups, potentially leads to incorrect species identification of the species, primarily due to overlapping morphologies and rarity of fruiting bodies (Tamm & al. 2010, Flores-Rentería & al. 2014, Saba & al. 2019). Our phylogeny clustered our ITS sequence in a distinct clade with two other *G. sumneriana* sequences ML support 100% (Fig. 1). One nucleotide separated our ITS sequence and the *G. sumneriana* sequence from Italy (position 114). Additional collections and sequences from *G. sumneriana* might indicate intraspecific variations in the ITS region (e.g., Nilsson & al. 2008). *Geopora ahmadii* (Saba & al. 2019), morphologically similar to our *G. sumneriana*, is phylogenetically separated in our analysis (Fig. 1). Morphologically, *G. ahmadii* differs from *G. sumneriana* by single oil drop per ascospore and shorter length (19–26.0 µm long in *G. ahmadii*). Saba & al. (2019) hypothesized (based on ascospore size and shape) that *G. arenosa* collected from Pakistan might represent *G. ahmadii*. This should be tested by morphological examination and sequencing of the type specimen, as it is of supreme importance to evaluate type material to evaluate whether the name-bearing type material is resembles or differs from newly collected samples (Dayarathne & al. 2016). Re-examination of type materials would definitely lead to more reliable identification of the species within *Geopora*.

In conclusion, informative field surveys and a combined approach involving thorough morphology and multi-locus phylogenetic analyses will help to resolve systematics and evolution of the species within *Geopora*.

Association of *Geopora* species with their ectomycorrhizal hosts, phenology, distribution, soil characteristics, and type specimens should also be studied to support correct species identifications.

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Didymocyrtis epiphyscia, Lichenochora weillii, and *Lichenoconium xanthoriae* newly recorded from Turkey

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Abstract—Three lichenicolous fungal species, *Didymocyrtis epiphyscia, Lichenochora weillii,* and *Lichenoconium xanthoriae,* are reported for the first time from Turkey. Comments on the taxonomy, ecology, and hosts and photographic illustrations are provided for each species.

Key words—biodiversity, lichens, *Lichenoconiaceae, Phaeosphaeriaceae, Phyllachoraceae*

Introduction

The lichenicolous fungi of Turkey have received increasing attention during the last fifteen years since Hafellner & John (2006) compiled the first checklist recognizing 63 taxa. Halıcı (2008) published an updated list and key for the 117 known taxa of lichenicolous *Ascomycota* (including mitosporic fungi), and subsequent papers have published new records (Halıcı & al. 2012; Kocakaya & al. 2016a, 2018, 2020) and new species (Kocakaya & al. 2016b, Hawksworth & al. 2016).

Among the c. 200 lichenicolous fungi species currently known from Turkey, *Lichenoconium* Petr. & Syd. is represented by six species, *Lichenochora* Hafellner by three species, and *Didymocyrtis* Vain. by one species (John & Türk 2017, Yazıcı & al. 2011). Here, I report the presence of three additional species from those genera and provide interesting information on their anatomy and ecology.

Material & methods

All specimens were collected in Çamlık National Park (Yozgat) during 2018–19. Çamlık National Park is Turkey's first National Park. As a national park, it is a well-preserved area, with oak (*Quercus pubescens*) and hawthorn (*Crataegus orientalis*) woods dominating the lower parts, while the higher elevations are occupied by *Pinus nigra* forests. Lichenicolous fungi are more common in preserved areas.

Vouchers are stored at the lichen herbarium of Yozgat Bozok University, Science and Art Faculty, Yozgat, Turkey, 66400 Yozgat, Turkey (YBUL); herbarium accession numbers are given in parentheses after locality details. Specimens were examined in water, 10% KOH, Lugol's, and Meltzer's iodine solutions. Spores were generally measured in water mounts. The specimens were examined with an Olympus SZX16 stereomicroscope and an Olympus BX53 light microscope. Micro- and macrophotographs were taken with an Olympus DP72 digital microscope camera with c-mount interface and with a 5-megapixel CCD.

New records

Didymocyrtis epiphyscia Ertz & Diederich,
Fungal Diversity 74: 71 (2015) Fig. 1a,b

Conidiomata superficial and aggregated on host apothecia, black, ≤150 µm. Conidiogenous cells ampulliform, aseptate, hyaline, 3–6 µm. Conidiospores simple, hyaline, ellipsoid, with usually one or two small guttules, 4–7 × 3.5–5 µm (n = 50). The lichenicolous fungus host apothecia blacken when infected (Fig. 1a).

Specimen examined—**TURKEY. Yozgat, Çamlık National Park**, 39°48′04″N 34°48′49″E, 1615 m, on apothecia of *Physcia stellaris* (L.). Nyl., 20 July 2019, M. Kocakaya MK-4114 (YBUL).

Comments—The Turkish specimen was found growing on the apothecia of *Physcia stellaris* on *Quercus* spp. Ertz & al. (2015) segregated *D. epiphyscia* s.lat. on *Physcia adscendens* and *P. tenella* from genetically related *D. epiphyscia* s.str. on *Physcia aipolia* based on consistently narrower conidia—3.7 –8.0 × 2.0–3.5 µm in *D. epiphyscia* s.lat. and 4.0–7.8 × 3.2–5.0 µm in *D. epiphyscia* s.str. Our specimen completely matches the description of *D. epiphyscia* s.str. (Ertz al. 2015).

Didymocyrtis epiphyscia has also been reported from other host genera, e.g., on *Physconia distorta* (Hawksworth 1981), *Phaeophyscia orbicularis* (Brackel 2011), and *Parmelia sulcata* (Brackel 2007, 2009; Zhurbenko & al. 2012). The species has previously been reported from Austria, France, Scotland, Luxembourg, and Canada (Ertz & al. 2015) as well as *Phoma physciicola* Keissl. from Russia (Zhurbenko & Tugi 2013).

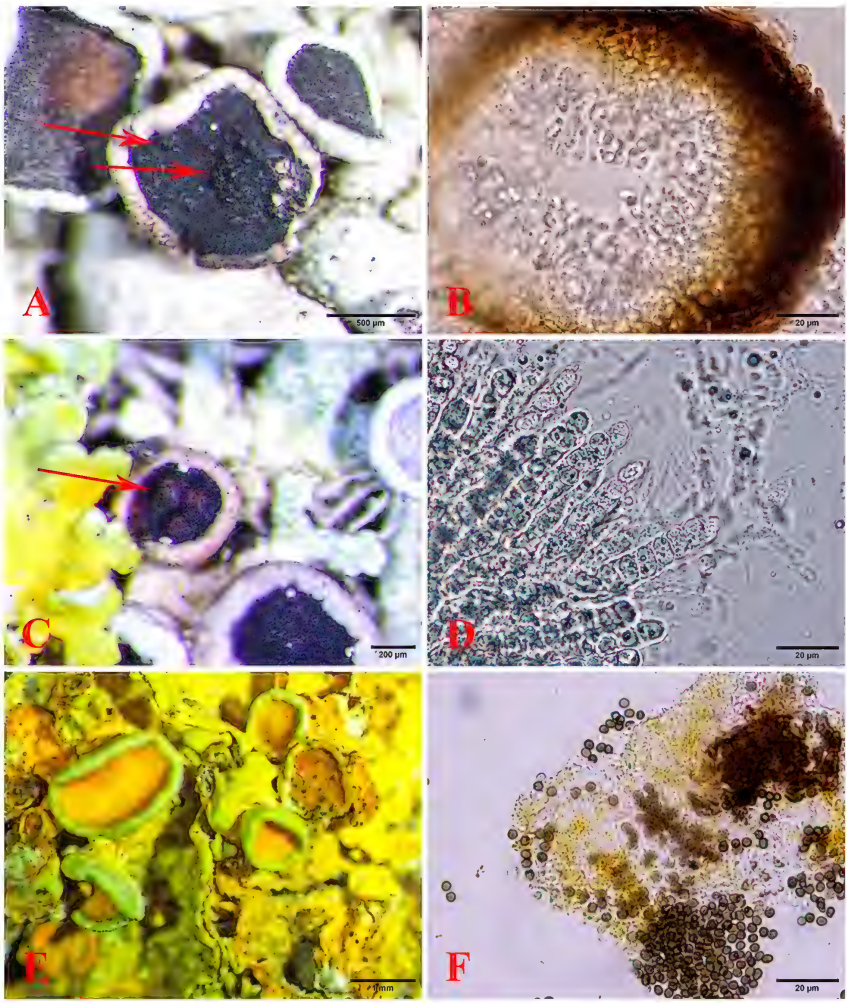

Fig. 1. ***Didymocyrtis epiphyscia*** (MK-4114): A. Perithecia on apothecia of *Physcia stellaris*; B: Conidia. ***Lichenochora weillii*** (MK-3822): C. Perithecia on *Physcia tenella*; D. Ascus and ascospores. ***Lichenoconium xanthoriae*** (MK-3830): E. Conidiomata on apothecia of *Xanthoria parietina*; F. Conidia.

The sole *Didymocyrtis* species previously reported from Turkey represents *D. foliaceiphila* (Diederich & al.) Ertz & Diederich, which differs by its narrowly ellipsoid conidia, immersed pycnidia, and *Cladonia* host (Ertz & al. 2015; Kocakaya & al. 2018).

Lichenochora weillii (Werner) Hafellner & R. Sant.,
Nova Hedwigia 48(3–4): 369 (1989) FIG. 1C,D

Perithecia subglobose to globose, immersed-subimmersed to erumpent in the ostiolar region, 150–200 µm, aggregated in groups. Ascus 8-spored, 70–100 × 10–16 µm (n = 20), with spores are organized in a single row in ascus. Ascospores hyaline, 1-septate, slightly constricted at the septum, smooth-walled, with many guttules in each cell, 9–12 × 7–9 µm (n = 60).

SPECIMENS EXAMINED—**TURKEY. YOZGAT, Çamlık National Park**, 39°48′02″N 34°48′46″E, 1635 m, on apothecia of *Physcia tenella* (Scop.) DC., 22 July 2018, M. Kocakaya MK-3822 (YBUL); 39°48′20″N 34°48′51″E, 1490 m, on apothecia of *Physcia* sp. 22 July 2018, M. Kocakaya MK-3860 (YBUL).

COMMENTS—Our specimens represent the first report of *L. weillii* on *Physcia* hosts. One Turkish specimen was collected from apothecia of *Physcia tenella* on *Acer* spp.; this host is quite common in Turkey (John & Türk 2017). Ascospore sizes vary in the species; they are cited as 7–11 × 5–6 µm by Werner (1937) but as 10–12 × 8–9.5 µm by Hafellner (1989); our specimen matches Hafellner's specimen more closely. Previous studies suggest that *Lichenochora weillii* always develops on *Physconia* spp. (Hafellner 1989; Gromakova 2018; Khodosovtsev & al. 2019), but all the characteristics of our specimens match the original description. *Lichenochora thallina* rarely develops on *Physcia,* but it has longer and narrower ascospores than *L. weillii* (Hafellner 1989). *Lichenochora weillii,* which was originally described by Werner (1937) from Spain, has also been reported from Belgium (Ertz & al. 2008), Svalbard (Zhurbenko & Brackel 2013), Sweden, North America (Hafellner 1989), and Ukraine (Gromakova 2018; Khodosovtsev & al. 2019).

Lichenochora species previously reported from Turkey include *L. aprica*, Hafellner & Nik. Hoffm., *L. atrans* Halıcı & al., and *L. verrucicola* (Wedd.) Nik. Hoffm. & Hafellner (John & Türk 2017, Yazıcı & Aslan 2019).

Lichenoconium xanthoriae M.S. Christ.,
Friesia 5(3–5): 212 (1956) FIG. 1E, F

Pycnidia immersed to erumpent, black, subglobose, (100–)150(–200) µm in diam.; conidiospores dark brown, simple, subglobose, almost smooth to slightly verruculose, 3–6 × 3–5 µm (n = 48). The lichenicolous fungus causes slightly whitening on the host apothecia and thallus (FIG. 1E).

SPECIMEN EXAMINED—**TURKEY. YOZGAT, Çamlık National Park**, 39°48′20″N 34°48′51″E, 1490 m, on apothecia of *Xanthoria parietina*, 22 July 2018, M. Kocakaya MK-3830 (YBUL).

Comments—The Turkish specimen was found growing on the apothecia of *Xanthoria parietina* on *Quercus* spp. The host of the type specimen is *Xanthoria parietina* (Christiansen 1956), but it has also been recorded on other unrelated lichen genera (Brackel 2008; Kocourkova 2000; Triebel & al. 1991). This species was previously reported from Austria (Etayo & Berger 2009), Italy (Brackel 2008), Russia (Himelbrant & al. 2013), and USA (Haldeman 2019).

Lichenoconium species previously reported from Turkey are *L. aeruginosum* Diederich & al., *L. erodens* M.S. Christ. & D. Hawksw., *L. lecanorae* (Jaap) D. Hawksw., *L. lichenicola* (P. Karst.) Petr. & Syd., *L. pyxidatae* (Oudem.) Petr. & Syd., and *L. usneae* (Anzi) D. Hawksw. (John & Türk 2017; Yazıcı & al. 2011).

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Ganoderma leucocontextum, a new record from Pakistan

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Abstract—*Ganoderma leucocontextum* is reported from Khyber Pakhtunkhwa province as a new record from Pakistan. This species in the *G. lucidum* complex is characterized by reddish brown to yellowish brown zones on the pileus. The Pakistani specimens are morphologically described and illustrated and their identification supported by a nrITS DNA based phylogeny.

Key words—coniferous, *Ganodermataceae*, polypore, taxonomy, temperate regions

Introduction

Ganoderma P. Karst. (*Ganodermataceae*, *Polyporales*) is a genus of c. 80 accepted species and has a world-wide distribution (Richter & al. 2015). *Ganoderma leucocontextum* is popularly known as a health-oriented herbal mushroom (Li & al. 2015; Wang & al. 2015) and commonly called 'Zanglingzhi' in Tibet Autonomous Region (Wang & al. 2015). The species contains numerous bioactive secondary compounds (Chen & al. 2018) that are pharmacologically valuable in America, Europe, and China due to their therapeutic effects (Xing & al. 2016). However, there has been little scientific research on *G. leucocontextum* due to its rarity (Wang & al. 2015).

Eight *Ganoderma* species have been reported from Pakistan: *G. colossus* (Fr.) C.F. Baker and *G. lucidum* (Curtis) P. Karst. (Ahmad 1956); *G. ahmadii* Steyaert, *G. applanatum* (Pers.) Pat., *G. flexipes* Pat., *G. resinaceum* Boud., and

G. tornatum (Pers.) Bres. (Ahmad 1972); and *G. tsugae* Murrill (Irshad & al. 2012). Here we report on a ninth species for the country, *G. leucocontextum*.

Materials & methods

Collection procedures

Samples were collected during the monsoon season (2018) in Pakistan. Macroscopical features (color, shape, surface texture, length, and width) were noted from fresh basidiomata, which were also photographed in the field. Samples were dried using a dehydrator and stored in sealed polythene bags.

Study sites

The specimens of *Ganoderma leucocontextum* were collected from Ayubia National Park, Khyber Pakhtunkhwa, District Abbottabad, and Naran Valley, District Mansehra, Pakistan. Ayubia National Park is located in the western Himalayas, north of Murree and south of Nathiagali (33°51′55″N 73°08′20″E). This area is covered by temperate broadleaf, mixed, and coniferous forest. The average minimum–maximum temperatures are 3–11 °C and the average annual rainfall is 1244 mm (Afza & al. 2018).

Naran Valley lies in northeastern District Mansehra (34°54.26′N 73°38.90′E). Its climate is dry temperate. Snowfall is heavy in the winter, but summers are cool and dry, and the temperature remains below 10 °C during the whole year (Khan & al. 2011).

Morphological characterization

The size, shape, and color of basidiomata were noted. Color descriptions follow Munsell (1975). Microscopic structures were observed from cross sections of tissues that were soaked in KOH (5% w/v), stained with Congo red (1 %), and viewed under a Meiji Techo MX4300H compound light microscope at 100× magnification. At least 30 measurements were made of all the microscopic features. For basidiospores, 50 measurements were taken and presented as length × width (Nagy & al. 2010).

DNA extraction, sequence alignment and molecular phylogeny

Total genomic DNA was extracted from the material following a modified CTAB procedure (Doyle & Doyle 1987). The nuclear ribosomal ITS region was amplified by using primers ITS1 and ITS2 (White & al. 1990). Reaction mixtures (20 µl) contained 0.5 µl template DNA, 8.5 ml distilled water, 0.5 µl of each primer, and 10 ml PCR mix [DreamTaqGreen PCR Master Mix (2X)]. Amplification conditions were 35 cycles of 95 °C for 30 s, 52 °C for 30 s and 72 °C for 1 min, with a final extension at 72 °C for 10 min. Amplified PCR products were purified and sequenced by Tsingke Co. Ltd.

The consensus sequence was generated from both ITS1 and ITS2 in BioEdit vers. 7.2.5 (Hall 1999) and then homology searches were performed at the NCBI web site using BLASTn. Sequences generated during this study were deposited in GenBank. A dataset of 35 ITS sequences (Table 1) from published literature was downloaded from GenBank. Sequences were aligned and edited using ClustalX 2.1

Table 1. *Ganoderma* and *Amauroderma* sequences used in the phylogenetic analysis.

Species	Origin	Voucher	GenBank No.	Reference
G. lingzhi	Japan	WD-2038	EU021456	Wang & al. 2009
	Japan	WD-565	EU021455	Cao & al. 2012
	China	Wu1006-38	JQ781858	Cao & al. 2012
	China	Cui9164	JQ781859	Cao & al. 2012
G. curtisii	USA	CBS 100131	JQ781848	Cao & al. 2012
	USA	CBS 100132	JQ781849	Cao & al. 2012
G. multipileum	China	Dai 9521	JQ781874	Cao & al. 2012
	Taiwan	BCRC 37043	EU021460	Wang & al. 2009
	India	BCRC 36123	EU021459	Wang & al. 2009
G. tropicum	China	Yuan 3490	JQ781880	Cao & al. 2012
	China	Dai 9724	JQ781879	Cao & al. 2012
	Taiwan	BCRC 37122	EU021457	Wang & al. 2009
G. flexipes	China	Wei 5494	JN383979	Cao & Yuan 2012
	China	Wei 5491	JQ781850	Cao & al. 2012
G. sichuanense	China	Cui 7691	JQ781878	Cao & al. 2012
	China	HMAS 42798	JQ781877	Cao & al. 2012
G. resinaceum	England	HMAS86599	AY884177	Li & al. 2015
	Italy	GrTO96	AM906065	Guglielmo & al. 2008
G. leucocontextum	China	GDGM44304	KJ027608	Li & al. 2015
	China	GDGM44303	KJ027607	Li & al. 2015
	China	GDGM44305	KJ027609	Li & al. 2015
	China	GDGM42932	KF372586	Li & al. 2015
	Pakistan	LAH36345	MK713839	This study
	Pakistan	LAH36346	MN134012	This study
G. valesiacum	Europe	CBS 282.33	Z37056	Moncalvo & al. 1995
G. ahmadii	Pakistan	FWP 14329	Z37047	Moncalvo & al. 1995
G. oregonense	USA	ATCC 46750	Z37061	Moncalvo & al. 1995
	USA	ATCC 46750	Z37061	Li & al. 2013
G. lucidum	Sweden	Dai 2272	JQ781851	Cao & al. 2012
	China	Dai 3937	JQ781853	Cao & al. 2012
	England	HMAS 86597	AY884176	Li & al. 2015
G. tsugae	England	CBS 223.48	Z37054	Moncalvo & al 1995
	England	AFTOL-ID 771	DQ206985	Moncalvo & al. 1995
A. rude	Taiwan	GDGM 25736	KF372587	Li & al. 2015

(Larkin & al. 2007) and BioEdit. These sequences were aligned with MAFFT v. 10 (http://mafft.cbrc.jp/alignment/server/index.html; Katoh & Standley 2013) and manually edited at 593 positions to generate a phylogenetic tree representing 15 taxa, with *Amauroderma rude* (Berk.) Torrend selected as outgroup. MEGA version 10.0 was used to run the maximum likelihood phylogenetic analysis with 1000 bootstrap replicates (Tamura & al. 2011); branches with less than 50% bootstrap support were collapsed.

Taxonomy

Ganoderma leucocontextum T.H. Li, W.Q. Deng, Sheng H. Wu, Dong M. Wang & H.P. Hu, Mycoscience 56(1): 82 (2015) FIGS 1–2

BASIDIOMATA stipitate, verrucose, zonate, inner zone maroon brown (5YR 4/8), outer zone yellowish brown (7.5YR 6/8), margins white; PILEUS 10–18 × 5–9 cm, 2–3 cm thick, glossy, shiny, smooth, reniform, dimidiate to flabelliform, margins thin, obtuse, white, radially wrinkled, blackish red-brown towards stipe (5YR 3/4), flesh soft with hard crust; STIPE 6–7 × 2–3 cm, cylindrical, slightly wrinkled, glossy, fibrous to woody, chocolate brown (5YR 3/4); PORES 114–153 × 222–255 µm, creamy to white, subcircular; TUBES 5–6 mm long, non-stratified, ochraceous (2.5YR 8/4); CONTEXT 2 cm thick, milky cream (2.5YR 8/4), dry, fibrous, corky.

HYPHAL SYSTEM trimitic, comprising 1) generative hyphae (septate, clamped, colorless, thin-walled), 2) skeletal hyphae (thick-walled, colorless, unbranched or few branches with distal end), and 3) binding hyphae (arboriform, colorless, thick-walled, multi-branched). BASIDIOSPORES 10.4–12.2 × 6.4–10.2 µm, broadly ellipsoid, rough, bitunicate; exosporium hyaline, non-pigmented, thick, brown, episporium verrucose, echinulae dark brown; eusporium, highly thick inter-walled pillars, apically truncate, myxosporium end tapered. CHLAMYDOSPORES 8.2–9.5 × 7.5–8.2 µm, broad, round, rough, pigmented, highly-ornamented. CRUSTOHYMENIDERM CELLS 30–58 × 9–11 µm, amyloid, thick-walled, clavate, originating from skeletal hyphae, brown; below cutis, thick brownish layer composed of hyaline generative and brown skeletal hyphae.

SPECIMENS EXAMINED—**PAKISTAN, KHYBER PAKHTUNKHWA, Abbottabad District**, Ayubia National Park, 34.0642°N 73.4072°E, elevation 2400 m a.s.l., gregarious on the older roots of *Pinus wallichiana* A.B. Jacks., 12 August 2018, Aisha Umar ANP1 (LAH36345, GenBank MK713839). **Mansehra District**, Naran Valley, 34.9093°N 73.6507°E, elevation 2450 m a.s.l., scattered in organic soil, on the roots of *Pinus wallichiana,* 20 September 2018, Aisha Umar AY2B (LAH36346, GenBank MN134012).

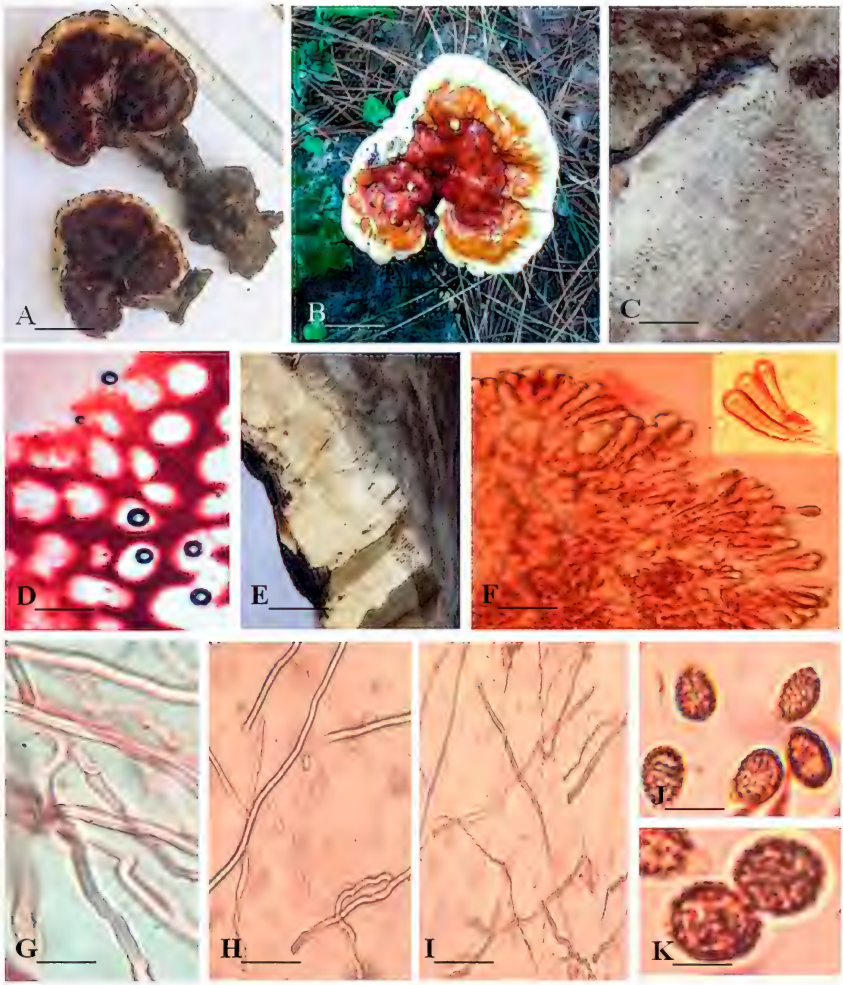

Fig. 1. *Ganoderma leucocontextum* (LAH36345). A, B. Basidiomata; C. Section of context; D. Lower surface pores; E. Section of context; F. Crusto-hymeniderm cells; G. Generative hyphae; H. Skeletal hyphae; I. Binding hyphae J. Basidiospores; K. Chlamydospores. Scale bars: A–C = 2 cm, D = 100 µm, E = 1 cm, G–I = 6 µm; F, J–K = 10 µm.

Molecular phylogeny

The ITS sequence analysis supported our specimen in *G. leucocontextum*. All sequences analyzed clustered in two clades supported by high bootstrap value (Fig. 3). In our tree, *G. leucocontextum* clusters in one clade representing

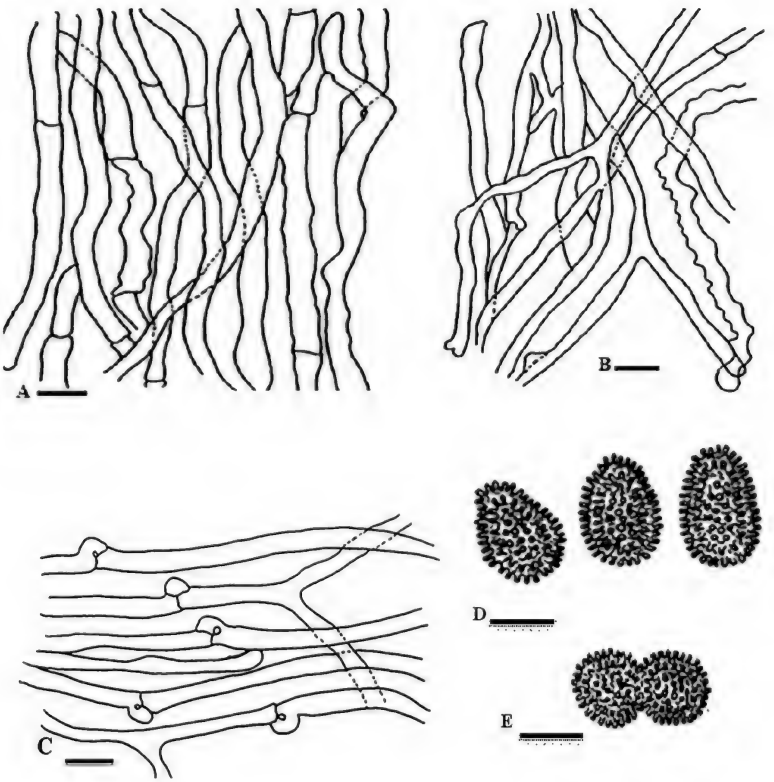

FIG. 2. *Ganoderma leucocontextum* (LAH36345). A, B. Binding and skeletal hyphae; C. Generative hyphae; D. Basidiospores; E. Chlamydospores. Scale bars: A–C = 5 µm; D, E = 10 µm.

G. lucidum, *G. oregonense* Murrill, *G. tsugae*, *G. ahmadii*, and *G. valesiacum* Boud. with 97% bootstrap value. Our specimens (ANP1, AY2B), which nested within the well-supported clade of *G. lucidum* complex, formed a discrete lineage with Chinese *G. leucocontextum* sequences (Li & al. 2015), supported by 96% bootstrap value (FIG. 3).

Discussion

Ganoderma leucocontextum was first described morphologically by Li & al. (2015) based on Chinese material. Our specimens (ANP1, AY2B) and the Chinese specimens both have creamy white context and a long thick

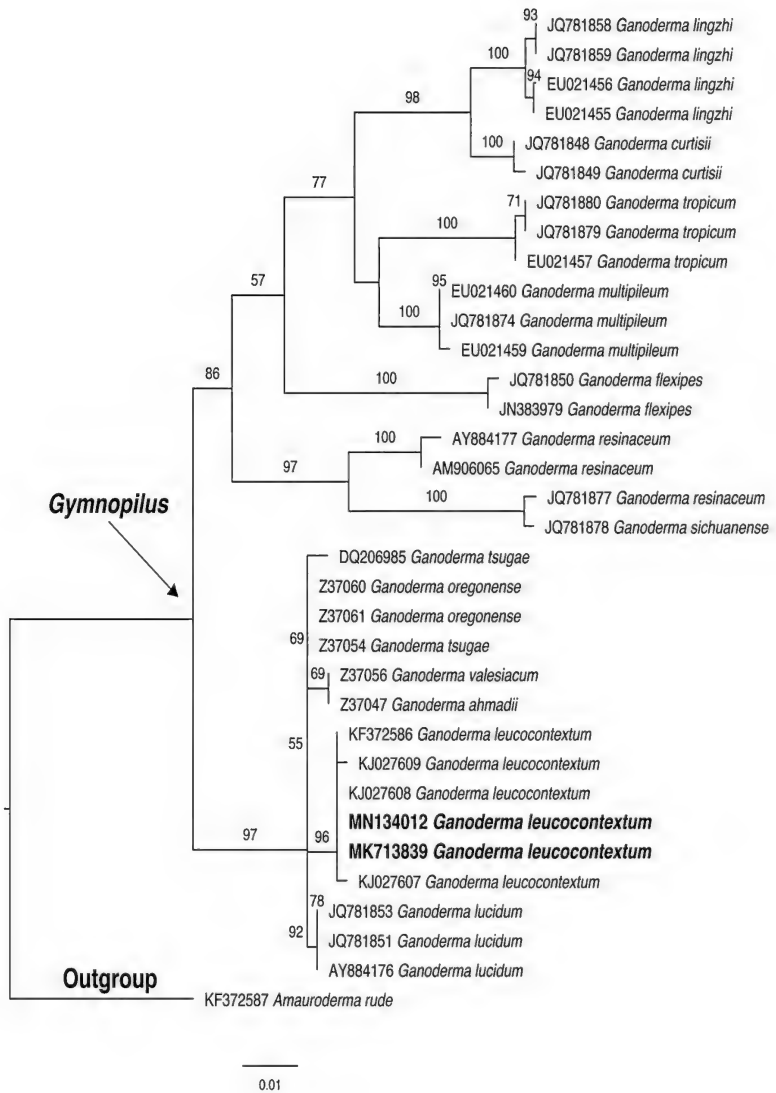

FIG. 3. Phylogenetic tree of *Ganoderma leucocontextum* and related species based on ITS sequences generated by maximum likelihood method in MEGA 10. *Amauroderma rude* was chosen as outgroup. Bootstrap values >50% are shown at the branches.

cylindrical stipitate fruiting body. The hymenophore pores (4–6 pores per mm) of the Chinese *G. leucocontextum* basidiomata were only slightly smaller and the Chinese crustohymeniderm cells (30–60 × 8–10 µm) were like those in Pakistani specimens. Basidiospore size and ornamentation of Pakistani specimens were also similar to those described for the Chinese *G. leucocontextum* (9.5–12.5 × 7–9 µm; Li & al. 2015).

The Pakistani material also possessed the trimitic hyphal system cited by Li & al. (2015) for *G. leucocontextum*. However, there was a significant difference in host association as the Chinese material was found on the base of dead wood stems of *Fagaceae* [*Cyclobalanopsis glauca* (Thunb.) Oerst.; Li & al. 2015], while our specimens (ANP1, AY2B) were found on the exposed older roots of *Pinaceae* [*Pinus wallichiana*].

The Pakistani *G. leucocontextum* basidiomata (ANP1, AY2B) also resembled *G. lucidum*, *G. oregonense,* and *G. tsugae*, but these species were easily distinguished based on microscopic characters and host habitat. The Chinese *G. leucocontextum* resembled East Asian *G. lucidum* (Li & al. 2015), but East Asian, European (Cao & al. 2012; Wang & al. 2012), and Chinese *G. lucidum* differed from one another based on molecular analysis (Yang & Feng 2013).

Ganoderma leucocontextum, *G. lucidum*, *G. oregonense*, and *G. tsugae* all produce hard basidiomata. Hong & al. (2001) suggested that wrinkles on the pileus surface, smaller basidioma size, and number of pores increase the hardness. *Ganoderma oregonense* basidiomata are reniform, flabellate, pulvinate sessile to laterally substipitate (Gilbertson & Ryvarden 1986), while our specimens possessed a long, thick, cylindrical, stipitate, laccate fruiting body as in *G. lucidum* and *G. tsugae.* The pileal surface color of *G. tsugae* (brown) and *G. lucidum* (reddish-brown) closely matched the Pakistani and Chinese *G. leucocontextum* (Cao & al. 2012) in contrast to the bay blackish brown color typical of *G. oregonense* (Steyaert 1980). Basidioma margins were white in both *G. tsugae* (Steyaert 1980) and *G. leucocontextum* whereas margins were folded (and thus brown) in *G. oregonense.*

The creamy context color in *G. leucocontextum* was close to the creamy to pinkish-buff context of *G. oregonense* (Zhou & al. 2015) and *G. tsugae* (Steyaert 1980). but dissimilar to the deep rusty brown context described for the European *G. lucidum* (Ryvarden & Gilbertson 1993). Pores are subcircular in *G. leucocontextum* and *G. lucidum* (Cao & al. 2012), circular in *G. tsugae,* and circular to irregular in *G. oregonense* (Steyaert 1980).

The 5–6 mm long tubes *G. leucocontextum* are virtually the same length as those cited for *G. lucidum* (5–7 mm). Highly echinulate ellipsoid spores of our specimens were larger than the echinulate ovoid spores of European samples of *G. lucidum* (7–12 × 6–8 µm; Wang & al. 2012) and smaller than the ovoid spores of *G. tsugae* (13–15 × 7.5–8.5 µm; Wasser & al. 2006, Hong & Jung 2004) and ovoid to ellipsoid in *G. oregonense* (11–12.5 × 7–8 µm; Zhou & al. 2015). The spore apex is convex in *G. tsugae*, collapsed in *G. lucidum*, and ellipsoid in *G. leucocontextum* and *G. oregonense*. The basidiospore color is light yellowish brown in both *G. oregonense* and *G. tsugae* and brown in *G. leucocontextum* and *G. lucidum* (Steyaert 1980). Trimitic hyphal system is present as in *G. lucidum*, *G. oregonense*, *G. tsugae* (El-Fallal & al. 2015) and our specimens of *G. leucocontextum*.

Ganoderma lucidum, *G. oregonense*, and *G. tsugae* associate only with conifers (Fernando 2008), whereas *G. leucocontextum* grows on both *Angiospermae* (China) and *Gymnospermae* (Pakistan).

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The authors are grateful to Prof. Dr. Abdul Nasir Khalid (Department of Botany, University of the Punjab) for providing all kinds of facilities during the study of this material. Thanks are due to Dr. Priyanka Uniyal (Government PG College, Gopeshwar, India) and Dr. Nousheen Yousaf (Government College University, Lahore, Pakistan) for presubmission review and helping the authors in many ways.

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Regional annotated mycobiota new to the Mycotaxon website

Abstract—Mycotaxon is pleased to add a new annotated species distribution list to our 144 previously posted free access fungae. The 49-page "Lichens from Brazil: a checklist of lichenized fungi from Acre, in the Amazon" by Aptroot, Santos, Oliveira, Cavalcante, and Cáceres may be downloaded from our website via http://www.mycotaxon.com/mycobiota/index.html

SOUTH AMERICA

Brazil

André Aptroot, Lidiane Alves dos Santos, Isaias Oliveira Junior, Janice Gomes Cavalcante, Marcela Eugenia da Silva Cáceres. Lichens from Brazil: a checklist of lichenized fungi from Acre, in the Amazon. 49 p.

Abstract—A checklist is presented with the 304 lichen species currently known from the state of Acre. Of these, 247 are corticolous species, 59 foliicolous species, and three (*Coenogonium confervoides, Echinoplaca pellicula,* and *Porina imitatrix*) grow on both substrata. All but 12 species are new reports based on identifications of material from our 2019 field trip to the Reserva Extrativista Cazumbá-Iracema near Sena Madureira. Additionally, 20 species are new records for Brazil, and two for the Neotropics.

Key words—biodiversity, *Graphis,* lichenized fungi, *Oellularia, Pyrenula,* tropical rain forest

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April–June 2021—Volume 136, p. 543

https://doi.org/10.5248/136.543

Regional annotated mycobiota new to the Mycotaxon website

Abstract—We are pleased to announce the posting of a new mycobiota on the Mycotaxon website: "Basidiomycete diversity within Calabrian pine (*Pinus brutia*) ecosystems on the island of Cyprus" by Michael Loizides. This brings to 146 the number of free access Fungae now available on http://www.mycotaxon.com/mycobiota/index.html

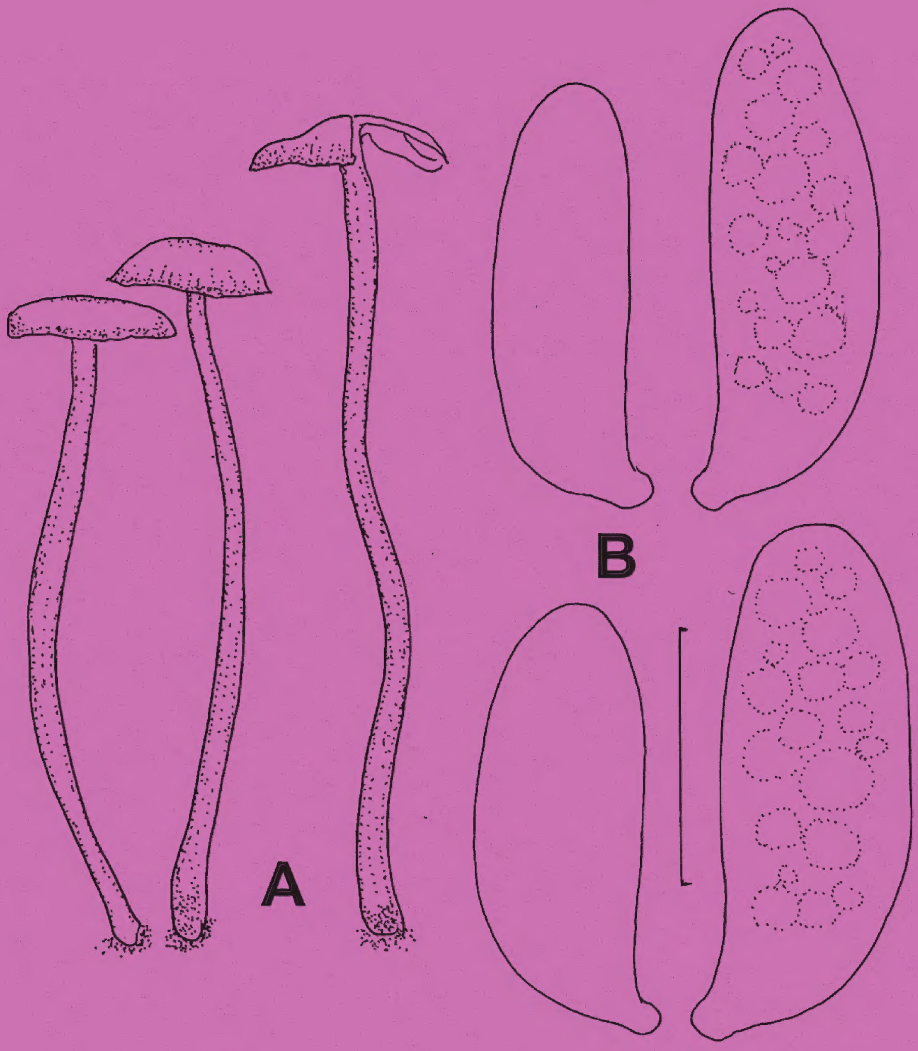
Europe

Cyprus

Michael Loizides. Basidiomycete diversity within Calabrian pine (*Pinus brutia*) ecosystems on the island of Cyprus. 28 p.

Abstract—Extended areas on the island of Cyprus including the vast majority of forested land, are occupied by *Pinus brutia,* an ecologically important tree forming ectomycorrhizal associations with a wide array of fungi. In this third installment of macromycete inventories from selected ecosystems in Cyprus, the basidiomycete diversity within *P. brutia* communities is reported following a 12-y-inventory. Two hundred and thirty-one taxa are compiled in an annotated checklist, 95 of which constitute new records for the country. Most notable of these are *Clitopilus daamsii, Hygrophorocybe nivea, Lepiota lepida, Leucoagaricus georginae, Rhodocybe matesina, Russula werneri, Tephrocybe striaepilea, Tephroderma fuscopallens,* and *Tricholoma chrysophyllum,* which are rarely reported in published literature. Notes on the altitude, phenology and estimated abundance are provided, accompanied by selected imagery and a review of previously published records.

Key words—biogeographical distribution, checklist, East-Mediterranean pine, fungi, island biogeography, Turkish pine



Collybiopsis filamentipes sp. nov.
(Petersen & Hughes— Fig. 14, p. 288)
Ronald H. Petersen, artist